

A REVISION OF THE ECHINONEMATINAE (NEMATODA: SEURATIDAE) FROM BANDICOOTS (MARSUPIALIA: PERAMELIDAE)

by LESLEY R. SMALES*

Summary

SMALES, L. R. (1997) A revision of the Echinonematinae (Nematoda: Seuratidae) from bandicoots (Marsupialia: Peramelidae). *Trans. R. Soc. S. Aust.* 121(1): 1-27, 30 May, 1997.

The name *Echinonema* being preoccupied the genus here designated *Linstowinema* (nom. nov.) is redescribed. The type species *L. cinctum* comb. nov. is synonymous with *E. neofidionalis* (sic) Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 but not with *E. cinctum sensu* Inglis, 1967, *sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *L. warringtoni* sp. nov. is established for *E. cinctum sensu* Yorke & Maplestone, 1926 and *sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *Linstowinema inglisi* comb. nov. is synonymous with *E. cinctum sensu* Inglis, 1967 and *E. inglisi sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 and is redescribed and four new species *L. latens* sp. nov., *L. tasmanianse* sp. nov., *L. maplestonei* sp. nov. and *L. peramelis* sp. nov. are described. All seven species can be differentiated as follows: *L. cinctum*, 14-18 rows of body hooks with undulating edges, oesophagus terminating at the level of the 8th-11th row; *L. warringtoni*, 9-13 rows of body hooks with undulating edges, oesophagus terminating at the level of the 9th-13th row; *L. inglisi*, 10-14 rows of body hooks with undulating edges, oesophagus terminating at the level of the 8th-9th row; *L. latens*, 9-11 rows of body hooks with undulating edges, oesophagus terminating posteriorly to the 11th row; *L. tasmanianse*, 13-15 rows hooks without undulating edges, oesophagus terminating at the level of the 8th-10th row; *L. maplestonei*, 12-13 rows of body hooks without undulating edges, oesophagus terminating posteriorly to 13th row of hooks; *L. peramelis*, 11-12 rows of body hooks without undulating edges, oesophagus terminating at level of the 12th row. A key to the species is given. *Linstowinema cinctum* occurs in *Isododon obesulus*, *I. macrourus*, *Perameles nasuta* and *P. gunnii*; *L. inglisi* and *L. tasmanianse* only in *I. obesulus*; *L. latens* only in *I. macrourus*; *L. warringtoni* in *I. macrourus*, *I. obesulus*, *I. auratus* and *P. nasuta*; *L. maplestonei* in *I. macrourus* and *P. nasuta* and *L. peramelis* only in *P. hoggainville*.

KEY WORDS: *Linstowinema*, Nematoda, Echinonematinae, *Isododon*, *Perameles*, bandicoots, Marsupialia.

Introduction

When Linstow (1898a) described a thorny headed nematode occurring in a bandicoot host, he called it *Hoplocephalus cinctus*. He subsequently found that *Hoplocephalus* was preoccupied so he renamed the genus *Echinonema* later in the same year (Linstow 1898b). *Echinonema* has continued to be used for the genus until the present. *Echinonema* also is preoccupied, however, having been used previously for a genus of sponges by Carter in 1881; I now propose the name *Linstowinema* nom. nov.

The bandicoot host originally was identified as *Perameles obesulus*. Linstow (1898a) described and figured a nematode with seventeen rows of hooks on the cuticular dilation of the oesophageal region of the body and oesophagus terminating on a level with the 9th row of hooks. Yorke & Maplestone (1926) described a nematode with 12-13 rows of body hooks and a relatively short oesophagus which they identified as "*E. cinctum*". They neither gave measurements nor provided a figure to show the relationship between the posterior end of the oesophagus and the rows of body hooks of their

specimens. Yorke & Maplestone (1926) assigned the type and, at that time only species, *L. cinctum* (Linstow, 1898), to the spirurid family Rictulariidae. Later Johnston & Mawson (1939) reported *L. cinctum* from a native cat, *Dasyurus viverrinus*, near Sydney and re-evaluated the available information on the host species. They concluded that Linstow's original description was based on material collected from *Isododon obesulus* (Shaw, 1797) from the Upper Burnett River in Queensland while Yorke & Maplestone's redescription was based on material from a bandicoot, possibly *I. macrourus* (Gould, 1842), collected in the vicinity of Townsville. Johnston & Mawson (1939) further concluded that both Linstow (1898a) and Yorke & Maplestone (1926) were describing material from the same host, namely, *I. macrourus*. Since *I. obesulus* does not occur in the Burnett River region (Braithwaite 1955) but *I. macrourus* does (Gordon 1955), this would seem to be a reasonable conclusion.

The first confirmed record of *Linstowinema* from the bandicoot genus *Perameles* Geoffroy, 1803 is by Johnston & Mawson (1940) from *P. nasuta* Geoffroy, 1804 collected near Sydney. These authors noted differences in the male tail of the specimens they examined, from earlier descriptions by Linstow (1898a) and Yorke & Maplestone (1926) but, nevertheless, assigned the specimens to *L. cinctum*.

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Of the differences noted by Johnston & Mawson (1940), the number of papillae on the male tail is problematic as neither they, Linstow (1898a) nor Yorke & Maplestone (1926) described the number and placement of papillae found on other specimens of *Linstowinema*. The expansion of the male body around the cloacal region described and figured by Johnston & Mawson (1940) is also a significant structure. Although not mentioned by Linstow (1898a), Yorke & Maplestone (1926) or Chabaud *et al.* (1980) in their descriptions of *L. cinctum*, it is comparable to the male tail described by Chabaud *et al.* (1980) for *Echinonema* sp. (*sic*) occurring in *P. nasuta* from an unknown locality.

No further work was done on the genus until Inglis (1967) re-examined the relationships of the superfamily Seuratoidea. He redescribed *L. cinctum* from material collected from *I. obesulus* near Perth and placed the sole genus within a new subfamily, the Echinonematinae, located within the seuratoid family Schneideriematidae on the basis of the form of the mouth opening, distribution of cephalic papillae, long spicules and short gubernaculum. Subsequently, the affinities of the genus were clarified by Quentin (1970) and the Echinonematinae included within the Seuratidae.

Chabaud *et al.* (1980) re-examined all the available material, established two new genera, *Seurechina* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 and *Inglechina* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 for worms from dasyurid marsupials and redefined *Echinonema* (now *Linstowinema*) and *E. cinctum* (*sic*) Linstow, 1898 *nee* Inglis, 1967. In their description of *L. cinctum* they noted difficulties in interpreting Linstow's original figure of 1898a, but decided that an oesophagus 1.8 mm long agreed with their definition of a "long" oesophagus, that is, one terminating at the level of the most posterior body hooks. Linstow's (1898a) figure clearly shows the oesophagus terminating at the level of the 9th of 17 rows of body hooks. Chabaud *et al.* (1980) also described three new species, namely, *E. edmondsi* (*sic*) from a dasyurid, *E. meridionalis* (*sic*) from *I. obesulus* and *E. inglisi* (*sic*) = *E. cinctum sensu* Inglis, 1967 also from *I. obesulus*. These authors also indicated that there were possibly additional species from the bandicoot genus *Perameles* but they had insufficient material for detailed descriptions.

The bandicoots (subfamily Peramelinae) are rabbit-sized omnivorous marsupials with long pointed heads and compact bodies. They forage by digging conical holes with their short forelimbs and explore these holes with their pointed snouts (Gordon & Hulbert 1989). *Perameles nasuta*, the long-nosed bandicoot, is found along the east coast of Australia, from rainforest in the north through

wetland and dry woodland to areas with little ground cover in the south (Stoddart 1995). Its distribution overlaps with *I. macrurus*, the northern brown bandicoot, which is found on the east coast, north of the Hawkesbury River and across the Northern Territory to the north of Western Australia, in areas of low ground cover including grassland, woodland and open forest (Gordon 1995). To the south, the distribution of *P. nasuta* overlaps that of *I. obesulus*, the southern brown bandicoot, which is found across southern Australia in Western Australia, South Australia and Victoria, southern coastal New South Wales and Tasmania and prefers sandy soils with scrubby vegetation or low ground cover that are burnt out from time to time (Braithwaite 1995). The eastern barred bandicoot, *P. gunnii* Gray, 1838, now restricted to Tasmania, where its distribution overlaps with that of *I. obesulus*, and a few relict colonies in southern western Victoria, prefers open grassland, but may also forage in scrub and heathland (Seebeck 1995). The western barred bandicoot *P. bougainville* Quoy & Gaimard, 1824, now existing only on Bernier and Dorre Islands Shark Bay, Western Australia was previously found across much of the southern half of Australia (Friend & Burbidge 1995). The only other bandicoot species still extant, *I. urralus*, the golden bandicoot, now survives only on Barron and Middle Islands off the coast of Western Australia, the north western Kimberley region and sub-humid parts of the Northern Territory, having been previously recorded from a much wider range of habitats (McKenzie *et al.* 1995).

In this study, all the available records and material collected from peramelids, including material dissected from hosts held in museum collections as well as live caught bandicoots, have been examined. This has provided sufficient material to reassess the taxonomic characters available to use for species discrimination, redesignate and redescribe the type species *L. cinctum* (Linstow, 1898) comb. nov. = *E. meridionalis* (*sic*) Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980, redescribe and name *L. warrigami* sp. nov. = *E. cinctum sensu* Yorke & Maplestone, 1926; *sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 and *L. inglisi* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1982 and distinguish the four additional new species from bandicoots that are described below.

Materials and Methods

Material and dissection records from 213 bandicoots were examined. This material was derived from three sources. Firstly, the gastrointestinal tracts of 56 bandicoots, collected between

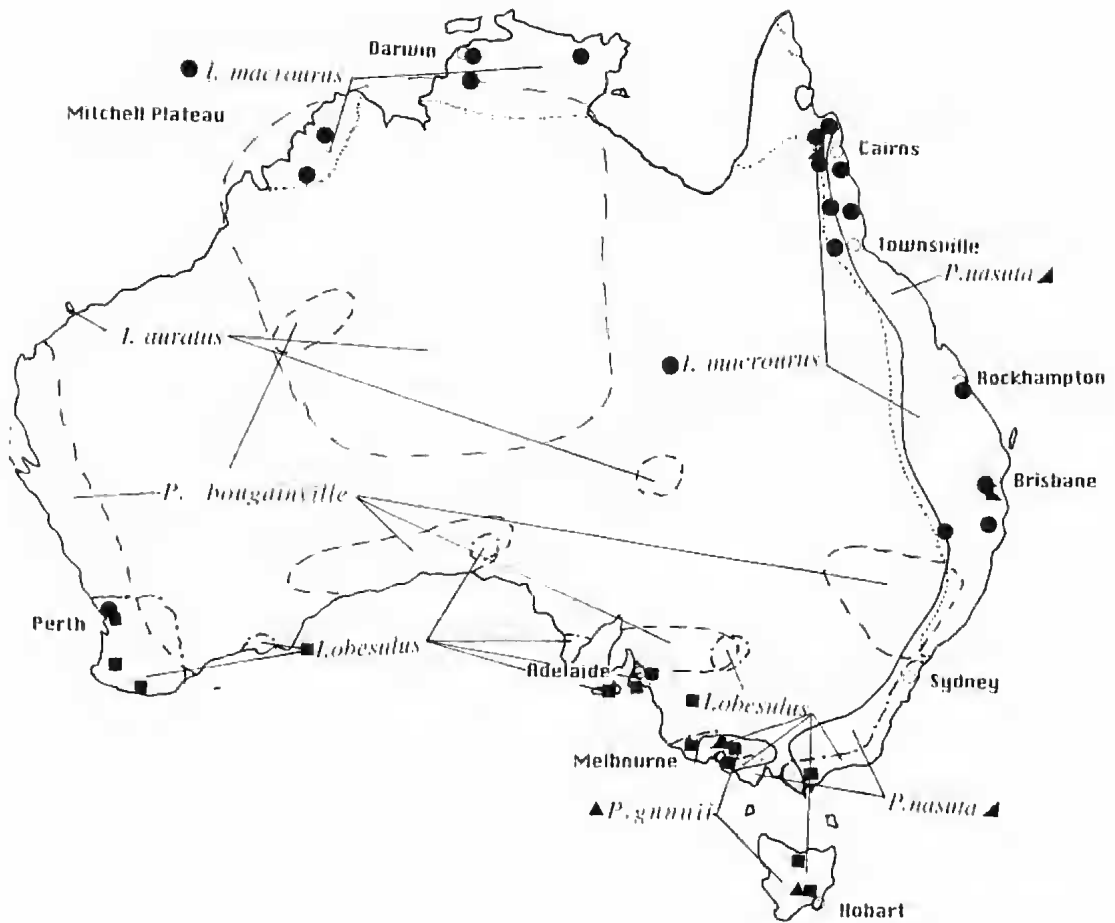


Fig. 1 Present and former distributions of Australian bandicoots (after Gordon & Hulbert 1989). The symbols indicate the localities where bandicoots were collected between 1989 and 1996. *Isodon auratus*, *I. macrourus*, ● *I. obesulus*, ■ *Perameles bougainville*, ▲ *P. gunnii*, ▲ *P. nasuta*, ▲.

1905 and 1988 and deposited in either the South Australian Museum (SAMA) or The Museum of Victoria (VM), were examined. These animals had probably been fixed in 5-10% formalin before being stored in 70% ethanol. The nematodes dissected from these hosts were stored in 70% ethanol. Secondly, 79 animals were either collected as fresh road kills or trapped alive, in spring-loaded wire box traps baited with peanut butter or a peanut butter, honey and oats mixture, between 1989 and 1996. The trapped animals were killed by intraperitoneal inoculation of euthanasia solution pentobarbitone sodium (Nembutal®). The digestive tract of each animal was examined under a dissecting microscope and any nematodes found were washed in normal saline, fixed in glacial acetic acid or hot or cold 10% formalin then stored in 70% ethanol. All the

available specimens of *Linstowinema* held in the Queensland Museum (QM), the Australian Helminthological collection of the SAMA (AHC), the Western Australian Museum (WAM), the CSIRO Division of Wildlife and Ecology (CSIRO) and The Natural History Museum, London (BM(NH)) were also examined. The preservation history of material from the former institutions is largely unknown but probably it was fixed in ethanol or formalin. Material from the CSIRO collection was fixed in hot 10% formalin. All material is now stored in 70% ethanol.

Specimens were examined from all the extant bandicoot species (number of bandicoots in parentheses) from 81 localities across Australia: *Isodon auratus* (5), *I. macrourus* (81), *I. obesulus* (85), *Perameles bougainville* (13), *P. gunnii* (6), *P. nasuta* (14), bandicoot, no species given (9). Host

TABLE 1. Distribution of bandicoot species examined for *Linstownema* species by State or Territory. Where no specific locality has been given in the dissection record the location is listed as Australia.

Abbreviations: A, Australia; WA, Western Australia; NT, Northern Territory; SA, South Australia including Kangaroo Island and Franklin Island; Q, Queensland; NSW, New South Wales; V, Victoria; T, Tasmania.

Species	Location							
	A	WA	NT	SA	Q	NSW	V	T
<i>Isodon auratus</i>	2	-	3	-	-	-	-	-
<i>I. macrourus</i>	2	2	13	-	50	14	-	-
<i>I. obesulus</i>	2	19	-	30	-	9	13	12
<i>Perameles bougainville</i>	13	-	-	-	-	-	-	-
<i>P. gunnii</i>	-	-	-	-	-	-	2	4
<i>P. nasuta</i>	1	-	-	-	7	4	2	-
bandicoot	1	-	-	-	8	-	-	-
	21	21	16	30	65	27	17	16

distributions and the locations of the 79 animals collected since 1989 are given in Fig. 1. Details of all the localities where specimens were collected are listed in the descriptions of species given below. Latitudes and longitudes are provided for all localities that are listed in the Australian Gazetteer. The location, by state, of all hosts species examined, is given in Table 1.

Specimens were examined after clearing in lactophenol or beechwood creosote. Measurements were made with the aid of an ocular micrometer or drawing tube and map measurer. Measurements are given in μm , as a range from 10 specimens followed by the mean in parentheses, unless otherwise stated. All the new material has been deposited in the AHC.

Comments on taxonomic characters

Prior to 1980 only one species was recognized in the genus *Linstownema* i.e. *Echinonema cinctum*. Then Chabaud *et al.* (1980) described four species, three from peramelid hosts and one from the dasyurid, *Dasyurus hallucatus* Gould, 1842. The species occurring in the dasyurid was distinguished from the others by having the first row of cephalic hooks longer than the second. The three species from bandicoots were differentiated from each other on the basis of the arrangement of hooks and spines on the body, the relative sizes and positions of papillae on the cloacal region, the relationship between the ventral spines and pre-cloacal papillae, the extent of small cuticular bosses surrounding the cloaca, the number of papillae on the tail of the male and the length of the oesophagus relative to the hooks on the dilated cuticular part of the anterior body associated with the region of the oesophagus.

Although Chabaud *et al.* (1980) recorded all the sensory organs on the male tail tip as pairs of papillae

Inglis (1967) had noted pairs of papillae and a pair of phasmids. Thus Inglis (1967) reported 3 pairs of papillae and a pair of phasmids on the tip of the tail of *Echinonema cinctum* (sic) and Chabaud *et al.* (1980) reported 4 pairs of papillae for the same species. Spicule morphology is uniform across the genus, differing only in total length and proportion of body length.

Chabaud *et al.* (1980) described the oesophagus as either "long", extending to the level of the last row of the body hooks or "short", terminating within the dilated cuticular region. Detailed examination of specimens for this study has shown that, although the termination of the oesophagus relative to the surrounding hooks is consistent within each species, the actual length of the oesophagus and its relationship to the body hooks may be difficult to determine. Specimens that are not completely straightened prior to or during fixation are problematic. It is difficult to tell the extent to which the oesophagus may have contracted into the neck region and the cuticle surrounding the oesophagus may also be contracted. Furthermore, the range of lengths of the oesophagus within populations of a species can also be quite variable, depending on the sizes and maturity of the worms being measured.

Both spines and hooks originate in the cuticle, but spines in this context, are defined as being small to tiny and rootless, whereas hooks consist of a thorn and a root anchoring the thorn within the cuticle. The smallest hooks may be only slightly larger than the largest spines. The relative lengths of the three rows of hooks on the cephalic bulb is a consistent character, but the dimensions of the hooks may vary markedly between individuals of the same species from the same individual host. Therefore hook dimensions are not useful for discriminating between species. The dimensions of the cephalic bulb are also

unreliable because of the potential variation caused by the extent of relaxation of the specimens prior to fixation and the method of fixation. Other consistent characters at the species level, however, are the number of rows of hooks on the dilated anterior body and the morphology of these hooks. In some species the roots of the hooks have undulating lateral edges giving them a "frilly" appearance; in others, the edges of the hooks are more or less plain.

Key to the species of *Linstowinema*

1. 1st row of cephalic hooks longer than 2nd row; parasites of dasyurids *L. edmondsi*
2nd row of cephalic hooks longer than 1st row; parasites of bandicoots (2)
2. Body hooks without undulating edges (3)
Body hooks with undulating edges (6)
3. Oesophagus terminates posterior to hooks on cuticular dilation of oesophageal region; male with 4 pairs of papillae, 1 pair of phasmids on tail tip (4)
Oesophagus terminates at or anterior to posterior row of body hooks on cuticular dilation of oesophageal region; male with 3 pairs of papillae, 1 pair of phasmids on tail tip (5)
4. Male with 8-10, female with 10-12 body hooks; male with 6 pairs cloacal papillae all same size, body spines extend along 90% of dorsal surface terminate at level of most anterior pair of lateral pre-cloacal papillae on ventral surface *L. latens*
Male with 11-13, female with 12-13 body hooks; male with 6 pairs of cloacal papillae, 1 pair lateral ad-cloacal papillae larger than other 5 pairs; body spines extend along 75% of dorsal surface terminate markedly anterior to cloacal papillae on ventral surface *L. maplestonei*
5. Male with ala-like expansions of body surrounding cloaca; with 6 pairs of cloacal papillae, 3 pairs of lateral cloacal papillae larger than 3 pairs of ventral cloacal papillae, spicule length about $\frac{1}{6}$ of body length; female with tail longer than 700 *L. tasmaniense*
Male without ala-like expansions of body, with 7 pairs cloacal papillae all same size, spicule length about $\frac{1}{16}$ of body length; female with tail shorter than 500 *L. peramelis*
6. Male with 13-16, female with 14-18 rows of body hooks; male with ala-like expansions of body surrounding cloaca, body spines terminate at level of most anterior pair of lateral pre-cloacal papillae on ventral surface *L. cinctum*

Male with 9-12, female with 11-14 rows of body hooks; male without ala-like expansions of body surrounding cloaca, body spines terminate markedly anterior to cloacal papillae on ventral surface (7)

7. Male with oesophagus shorter than 1570, female with oesophagus shorter than 1850, male with 6 pairs of cloacal papillae, pair of lateral ad-cloacal papillae larger than other 5 pairs, 3 pairs of papillae, 1 pair of phasmids on tail tip, spicule length about $\frac{1}{15}$ of body length; female with tail shorter than 940 *L. inglisii*
Male with oesophagus longer than 1570, female with oesophagus longer than 1860; male with 6 pairs of cloacal papillae all same size, 4 pairs of papillae, 1 pair of phasmids on tail tip, spicule length about $\frac{1}{20}$ of body length; female with tail longer than 980 *L. swarringtoni*

Systematics

Order Ascaridida

Superfamily Securatoidea

Family Securidae

Subfamily Echinonematinæ

Genus *Linstowinema* nom. nov.

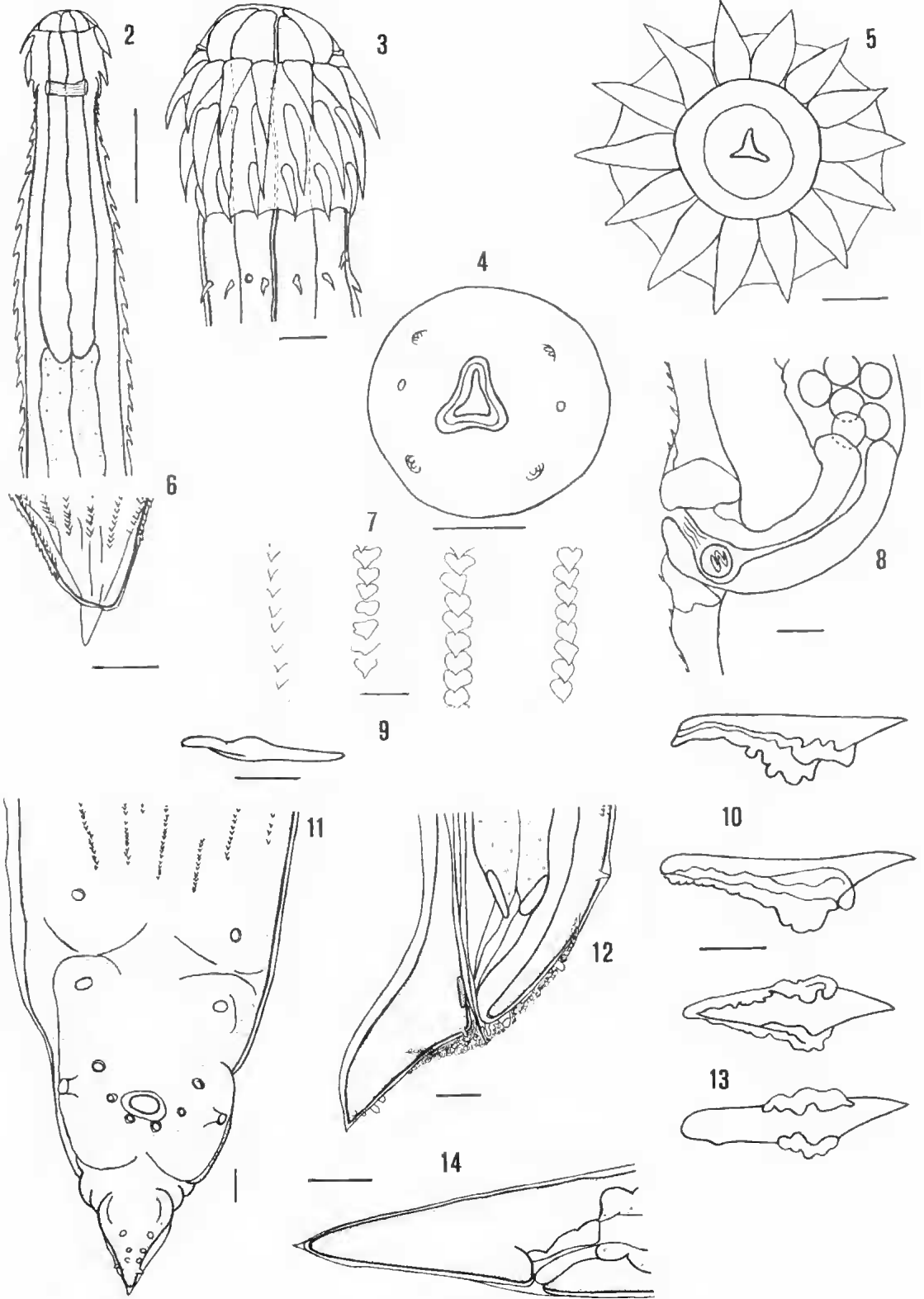
Type species: Linstowinema cinctum (Linstow, 1898) comb. nov.

Synonyms: *Hoplcephalus cinctus* Linstow, 1898, *Echinonema meridionalis* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 *nee Echinonema cinctum sensu* Yorke & Maplestone, 1926; Inglis, 1967; Chabaud, Seureau, Bain & Durette-Desset, 1980 (in part).

Linstowinema (nom. nov.)

Generic diagnosis

Anterior end with cephalic bulb bearing 3 rows of 14-16 files of large hooks. Mouth opening triangular in outline, without lips or lip-like structures, with 4 pairs double cephalic papillae, 1 pair amphids, inner circle of sense organs on edge of mouth (see Inglis, 1967, Figs 6, 7). Neck with 2-11 rows of very tiny spines. 8-18 rows of 14-16 hooks surround an anterior cuticular dilation, associated with oesophageal region. Body with numerous rows of spines, number of files of spines increasing progressively towards mid body, decreasing towards posterior, continuing to caudal tip of female, terminating at about $\frac{2}{3}$ of length dorsally, anterior to cloaca ventrally on male. Short oesophagus simple, club shaped, surrounded by nerve ring at level of cephalic bulb. Deirids simple, conical, at level of 1st row of cervical hooks. Spicules long, equal, identical; small gubernaculum present. Vulva at mid-



region of body; monodelphic ovejector directed anteriorly. Parasites of Australian dasyurid and peramelid marsupials.

Linstowinema cinctum (Linstow, 1898) comb. nov.
(FIGS 2-14)

Synonyms: *Hoplocephalus cinctus* Linstow, 1898a: pp. 469-471, Figs 3-11. *Echinonema meridionalis* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980: pp. 436-438, Figs 4, 5A, D; Spratt, Beveridge & Walter, 1991: p. 26. *Echinonema cincta* Linstow, 1898b: p. 672; Johnson & Mawson, 1940: pp. 473-474, Fig 25; *nee* Yorke & Maplestone, 1926; *nee* Inglis, 1967; *nee* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *Echinonema cincta* Mackerras, Mackerras & Sanders, 1953: p. 62, *Echinonema* sp. 2. Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980: p. 438, Fig. 5C, F; Spratt, Beveridge & Walter, 1991: pp. 23, 24 (in part).

Material examined

From *Isoodon obesulus* New South Wales: 1♀, fragment Lismore, (28° 49'S, 153° 16'E), April, 1965, AHC 4413. 4♂♂, Timbillica State Forest, (37° 19'S, 149° 43'E), 15.xii.1978, CSIRO N733; 14♂♂, 19♀♀, Sidlings Swamp North, Timbillica State Forest, (37° 17'S, 149° 45'E), 19.vii.1994, 17.iii.1994, 20.vii.1994, 23.iii.1994, CSIRO N4213, N4074, N4228, N4075; 85♂♂, 88♀♀, Sidlings Swamp South, Timbillica State Forest, (37° 18'S, 149° 45'E), 14.vii.1994, 20.vii.1994, CSIRO N4212, N4230.

From Victoria: 2♂♂, 14♀♀, Melbourne, (37° 47'S, 136° 59'E), 9.ix.1991, AHC 30292; 2♀♀, Monash University, (37° 47'S, 136° 59'E), no date, AHC 30293, 30294; 2♂♂, 2♀♀, Gorge Forest Road, (38° 21'S, 141° 36'E), Sept. 1962, AHC 30296; 2♂♂, 11♀♀, 7 fragments, no locality, no date, AHC 30295, 30298.

From South Australia: 1♂, 8♀♀, 6 anterior ends, Waitpinga, (32° 36'S, 138° 32'E), no date, AHC 4460; 3♂♂ 7♀♀, Scott Creek, (35° 04'S, 138° 42'E), 5.x.1992, AHC 30291; 3♂♂, 3♀♀, Myponga, (35° 23'S, 138° 28'E), May 1966, AHC 4446; Kangaroo Island, South Australia: 1♂, 2♀♀, Cape Willoughby, (35° 51'S 138° 08'E) 13.x.1990, AHC 30301; 2♀♀, Seal Bay, (36° 00'S, 137° 20'E), 4.i.1987, AHC 30304; 2♂♂, 2♀♀, Binowie, (37°

47'S, 136° 59'E), 5.viii.1987, AHC 30303.

From *Perameles gunnii* Tasmania: 6♂♂, 14♀♀, 4 fragments, Grove, (42° 59'S, 147° 07'E), AHC 30025; 3♂♂, 4♀♀, Kingston, (42° 59'S, 147° 18'E), 11.vii.1992, AHC 30056, 30057, 30058.

From *Perameles nasuta*: Queensland: 2♀♀, Wongabel State Forest, (17° 20'S, 145° 30'E) 9.vii.1982, CSIRO N1753; 1♀, Mt Nebo Road, (27° 23'S, 152° 47'E) 11.viii.1993, AHC 30316. New South Wales: 1♂, Epping, (33° 46'S, 151° 05'E), 11.viii.1993, AHC 30316; 1♂ Epping, (33° 46'S, 151° 05'E), 14.vii.1933, QM GL 12048; 3♂♂, 2♀♀, Sydney, (33° 50'S, 151° 15'E), no collection data, AHC 1820; 1♀, Nadgee State Forest, (37° 26'S, 149° 54'E), 13.ii.1978, CSIRO N493.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) files of hooks. 2nd row longest. 3rd row shortest (Fig. 3); neck with 5-9 rows of tiny spines; cuticular dilation of oesophageal region bearing 13-18 rows of 14 (male) (Fig. 2) or 16 (female) files of body hooks; 1st and last rows smallest, 4th-7th rows largest; roots of hooks with undulating edges (Figs 10, 13); remainder of body with up to 36 (male) or 54 (female) small spines at each annulation, over whole body of female; extending over $\frac{3}{4}$ of dorsal surface, terminating about 400 anterior to cloaca, almost reaching level of anterior pair of caudal papillae, on ventral surface of male body (Fig. 7). Oesophagus simple, club shaped, terminating about level with 8th - 11th row of hooks, within the anterior cuticular dilation; $\frac{1}{8}$ to $\frac{1}{10}$ body length (Fig. 2). Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male: Length 12-22 (14.8) mm, width 460-730 (600), Cephalic bulb 260-490 (395) long by 325-420 (380) wide; cephalic hooks 1st row 145-225 (170), 2nd row 170-235 (200), 3rd row 104-145 (130) long. Oesophagus 1445-2040 (1790) long, cuticular dilation bearing 13-16 rows body hooks. Deirids 520-630 (590), nerve ring 320-420 (375), secretory-excretory pore 500-530 (550) (n=3) from anterior end. Spicules equal, similar, without alae, 935-1150 (1035) long, about $\frac{1}{14}$ body length. Gubernaculum short, simple, subtriangular 60-63 (n=5) long (Fig. 9). Nine pairs caudal papillae; 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively,

Figs 2-14. *Linstowinema cinctum* (Linstow, 1898). 2. Anterior end, optical section (lateral view). 3. Cephalic end (lateral view). 4. Cephalic end (*en face* view). 5. Cephalic end male, optical section at level of first row of hooks (*en face* view). 6. Female tail tip (lateral view). 7. Male posterior body spines (ventral view). 8. Vagina (lateral view). 9. Gubernaculum (lateral view). 10. Body hooks (lateral view). 11. Male tail (ventral view). 12. Male tail (lateral view). 13. Body hooks (lateral view). 14. Female tail (lateral view). Scale bars = 500 µm 2; 100 µm 3, 4, 5; 50 µm 6, 8, 11, 12; 25 µm 7, 9, 10, 13; 250 µm 14.

1 pair lateral ad-cloacal, 2 pairs lateral pre-cloacal; all same size, 3 pairs papillae, pair phasmids well posterior to cloaca, near tail tip (Fig. 11). Cloacal region with small cuticular bosses; aka-like expansion of body anterior and posterior to cloaca (Fig. 11). Tail 310-450 (365) long (Fig. 12).

Female: Length 16-22 (20) mm, width 800-1035 (880). Cephalic bulb 455-580 (505) long by 455-600 (500) wide; cephalic hooks 1st row 180-235 (210), 2nd row 220-265 (245), 3rd row 130-180 (155) long. Oesophagus 1785-2125 (1900) long; cuticular dilation bearing 14-18 rows body hooks. Deirids 450-780 (625), nerve ring 440-520 (470), secretory-excretory pore 520, 585 (n=2) from anterior end. Vulva 7140-10370 (8830) from anterior end (Fig. 8). Vagina about 300 long (n=1). Tail 985-1120 (1050) long (Figs 6, 14). Eggs ovoid, 45-54 (48) long by 36-51 (43) wide.

Type host

Perameles nasuta Geoffroy, 1804

Type locality

Sydney, Australia

Site in host

Small intestine

Type specimen

Neotype AHC 1820

Remarks

The present location of the material described by Linstow as *Hoplocephalus* then renamed *Echinonema* is unknown. Yorke & Maplestone (1926) and Chabaud *et al.* (1980) neither gave a location for the type material nor indicated whether they had examined it. Linstow was working in Göttingen in 1898 but neither *Echinonema* nor *Hoplocephalus* is listed under specimens held in the Zoologisches Museum der Humboldt Universität, Berlin. This Museum does, however, list holdings of other type specimens from Linstow. The specimens are not held in the parasite collections of the BM (NH), the International Institute of Parasitology, St Albans, or the US National Museum Parasite Collection in Beltsville.

The type host was given by Linstow (1898a) as *Perameles obesulus*, one of two bandicoot species collected by Richard Semon. These species were identified by Romer (1901), using the catalogue of Thomas (1888) in the British Museum, as *Perameles obesulus*, from Burnett River and *P. macrura* from Cooktown, with measurements being given for *P. macrura*. *Perameles macrura* is formally listed as a synonym of *Isodon macrurus* (Mahoney & Ride

1988) but *P. obesulus* is not. This is surprising because the taxonomic status of *P. obesulus* was discussed by Mackerras & Mackerras (1960) who indicated that *Perameles obesula* = *Didelphis obesula* = *Isodon obesulus*, but that since the northern limit of distribution of *Isodon obesulus* is near Sydney, bandicoots recorded as *I. obesulus* from Queensland should be referred to as *I. macrurus*, the species occurring from north Queensland to northern New South Wales.

Yorke & Maplestone (1926) list the type host as *Perameles obesula*. Johnston & Mawson (1939) decided that since Yorke & Maplestone had drawn an original figure their material came from Townsville, in northern Queensland and stated that Linstow's material from *Isodon obesulus* came from Upper Burnett River also in Queensland. On that basis, Chabaud *et al.* (1980) concluded that the host of both the Linstow material and the Yorke & Maplestone material was *Isodon macrurus*, the northern brown and not *I. obesulus*, the southern brown bandicoot.

This does not, however, explain why Romer (1901) in his identification of the bandicoots collected by Semon lists them as two separate species rather than as *Perameles macrura* now *Isodon macrurus*. The catalogue of Thomas (1888) however, does list *P. nasuta*, so the Upper Burnett River bandicoots were probably *I. macrurus*.

Chabaud *et al.* (1980) noted that 1.8 mm, the measurement given for the length of the oesophagus by Linstow (1898a), was similar to measurements of specimens examined by them that had been collected from *I. macrurus* from northern New South Wales through to northern Queensland. In particular, these specimens had the oesophagus terminating at about the level of the posterior end of the cuticular dilation, a character they described as a 'long oesophagus'. Yorke & Maplestone (1926) did not indicate the length of the oesophagus relative to the rows of body hooks on the cuticular dilation but they described 12 or 13 'circles' of 14 to 16 rows of hooks. Two specimens collected by Nicoll in 1915, currently held in the BM(NH), which could possibly be the material described by Yorke & Maplestone (1926) and redescribed below also have the 'long oesophagus' described by Chabaud *et al.* (1980). The specimens described by Linstow (1898a) are drawn and labelled as having 17 'circles' of hooks with the oesophagus terminating at the level of the 9th row of hooks. These characters are consistent, not with *E. cinereum sensu* Chabaud *et al.* (1980) but with specimens described by Chabaud *et al.* (1980) as *E. meridionalis*, occurring in the southern brown bandicoot *Isodon obesulus* collected in South Australia.

In a re-examination of the material described by Chabaud *et al.* (1980) as *E. meridionalis*, together

with specimens collected from long-nosed and barred bandicoots for this study, it was found that all specimens had 14-18 rows of body hooks and the oesophagus terminated at the level of the 8th-11th row of hooks. Measurements of the oesophagus ranged from 1445 to 2040 for males and 1785 to 2125 for females, also consistent with the measurements given by Linstow (1898a).

Johnston & Mawson (1940) described three females and two males obtained from the intestine of the long nosed bandicoot *P. nasuta* collected in Sydney and attributed these to *E. cinctum*. They described and figured differences in the male tail, namely an expansion of the body surrounding the cloaca, similar to, but not transparent, as are caudal alae Chabaud *et al.* (1980) figured the posterior end of a male which they designated *Echinonema* sp. 2 from *P. nasuta* registered in the AHC as 1820. They commented that their specimens were comparable with those described by Johnston & Mawson (1940). Neither group described the anterior ends of the worms they examined. The only material registered in the SAMA which might be the original Johnston & Mawson specimens is AHC 1820. The morphology of the anterior ends of these worms, 13-18 body hooks, the oesophagus terminating level with the 9th-11th row of hooks, is consistent with *E. meridionalis sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980.

Chabaud *et al.* (1980) did not comment on the presence or absence of an expansion to the cloaca on their specimens but contrast *E. meridionalis* with *Echinonema* sp. 2 (see Chabaud *et al.* 1980, p. 438, Fig. 5) stating that *Echinonema* sp. 2, was comparable with the Johnston & Mawson (1940) description.

A re-examination of all the available specimens of *E. meridionalis* (*sic*) and *Echinonema* sp. 2 (*sic*) has failed to show any significant differences between them. Such differences as do exist can be attributed to the fact that Chabaud *et al.* (1980) were dealing with a mixed infection of two species, namely *L. cinctum* and *L. warringtoni* (described below) occurring in the material collected from Waitpinga and Myponga. The male *L. cinctum* in this population were at the small end of the size range and oesophageal length varies with worm length and maturity.

The description by Linstow (1898a) of *H. cinctus* is congruent with the revised description of material designated *E. meridionalis* by Chabaud *et al.* (1980). The description by Yorke & Mapleston (1926) of specimens from *L. macrurus* and identified as *E. cinctus*, is congruent with *E. cinctum sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 *non* Linstow, 1898. Therefore, I designate a specimen from AHC 1820 as the neotype of *L. cinctum*.

Linstowinema cinctum (Linstow, 1898) most closely resembles *L. inglisi* (redescribed below) in that the oesophagus is relatively short in relation to the number of rows of hooks, ending within the cuticular dilation. The males of both species have 3 pairs of caudal papillae and spicules $1/11-1/15$ body length. *Linstowinema cinctum* can be distinguished from *L. inglisi* in having 13-16 (male) and 14-18 (female) body hooks compared with 10-12 and 12-14 in *L. inglisi*. Although the oesophagus is relatively short it is, however, longer than in *L. inglisi*, being $1/6$ body length in male *L. cinctum* compared with $1/11$ body length in *L. inglisi*. The pair of lateral adcloacal papillae is no larger than the other pairs of ventral papillae in *L. cinctum* but is larger in *L. inglisi* (see Inglis 1967 Fig. 9). The ala-like expansion of the body surrounding the cloaca of *L. cinctum* is not found on *L. inglisi* (see Inglis 1967 Fig. 9). The body spines of *L. cinctum* only cover $1/4$ of the dorsal body surface but cover $3/10$ of the dorsal body surface of *L. inglisi*. Eggs of *L. cinctum* differ from those of all other species in that they are ovoid rather than almost spherical.

The material from *L. obesulus* from South Australia described by Chabaud *et al.* (1980) as *L. meridionalis* was found to be a mixed infection of *L. cinctum*, (females with up to 18 rows of body hooks, oesophagus terminating at about the level of the 9th-11th row) and *L. warringtoni* (females with up to 13 rows of body hooks, the oesophagus terminating about the level of the 10th-13th row) described below. A comparison of the measurements given by Chabaud *et al.* (1980) and the specimens examined for this study reveal that the males they measured were smaller in size, the oesophagus, spicules and tail were shorter than in the specimens examined for this study. The females, however, were within the same size range as for this study and the comparative measurements are more consistent.

The material dissected from the southern brown bandicoot collected at Scott Creek included some females up to 36 mm long. These were larger than the specimens from South Australia studied by Chabaud *et al.* (1980), (up to 27 mm long), from eastern barred bandicoots from Tasmania, (up to 22 mm long), and from long-nosed bandicoots, from Tasmania, (30-32 mm long). Other variations observed between female specimens collected in different hosts and localities in the present study and those of Chabaud *et al.* (1980) included the oesophagus longest in southern brown bandicoots from Scott Creek (1853-2380), and shortest in southern barred bandicoots from Myponga and Waitpinga (1100); the tail longest in eastern brown bandicoots from Tasmania (986-1122) and shortest in southern brown bandicoots from Scott Creek (884-986), and the vulva slightly more posterior

(10,030-14,450) in southern brown bandicoots from Scott Creek than in eastern barred bandicoots from Tasmania (7140-10,370) or southern brown bandicoots from Waitpinga (10,800). The eggs from the Scott Creek specimens were smaller than those from Waitpinga or Tasmania, being 33 by 36, 32 by 45, and 43 by 48 respectively. These differences could be either variations between populations within the species, or the result of contraction during fixation.

Linstowinema cinctum, originally described as occurring in *P. obesula* (sic) from Queensland is now recorded as also occurring in *I. obesulus*, *P. nasuta* and *P. gunnii*. The geographical range now includes Victoria, New South Wales, South Australia, including Kangaroo Island, and Tasmania as well as northern and southern Queensland. The record of *I. cinctum* in *I. obesulus* from Lismore, New South Wales, AHC 4413 is a dubious host record because the southern brown bandicoot is not found nearly as far north as Lismore (Braithwaite 1995). In all probability the host was *I. macrourus*.

Linstowinema warringtoni sp. nov.
(FIGS 15-24)

Synonyms: *Echinonema cincta* sensu Yorke & Maplestone, 1926: pp. 347-348 *nee* Linstow, 1898; *nee* Inglis, 1967; *sensu* Munday & Green, 1972: p. 10 (in part); *sensu* Chabaud Seureau, Beveridge, Bain & Durette-Desset, 1980: p. 435-436 (in part); *sensu* Spratt, Beveridge & Walter, 1991: p. 25 (in part). *Echinonema emeryi* sensu Johnston & Mawson, 1952: p. 33.

Material examined

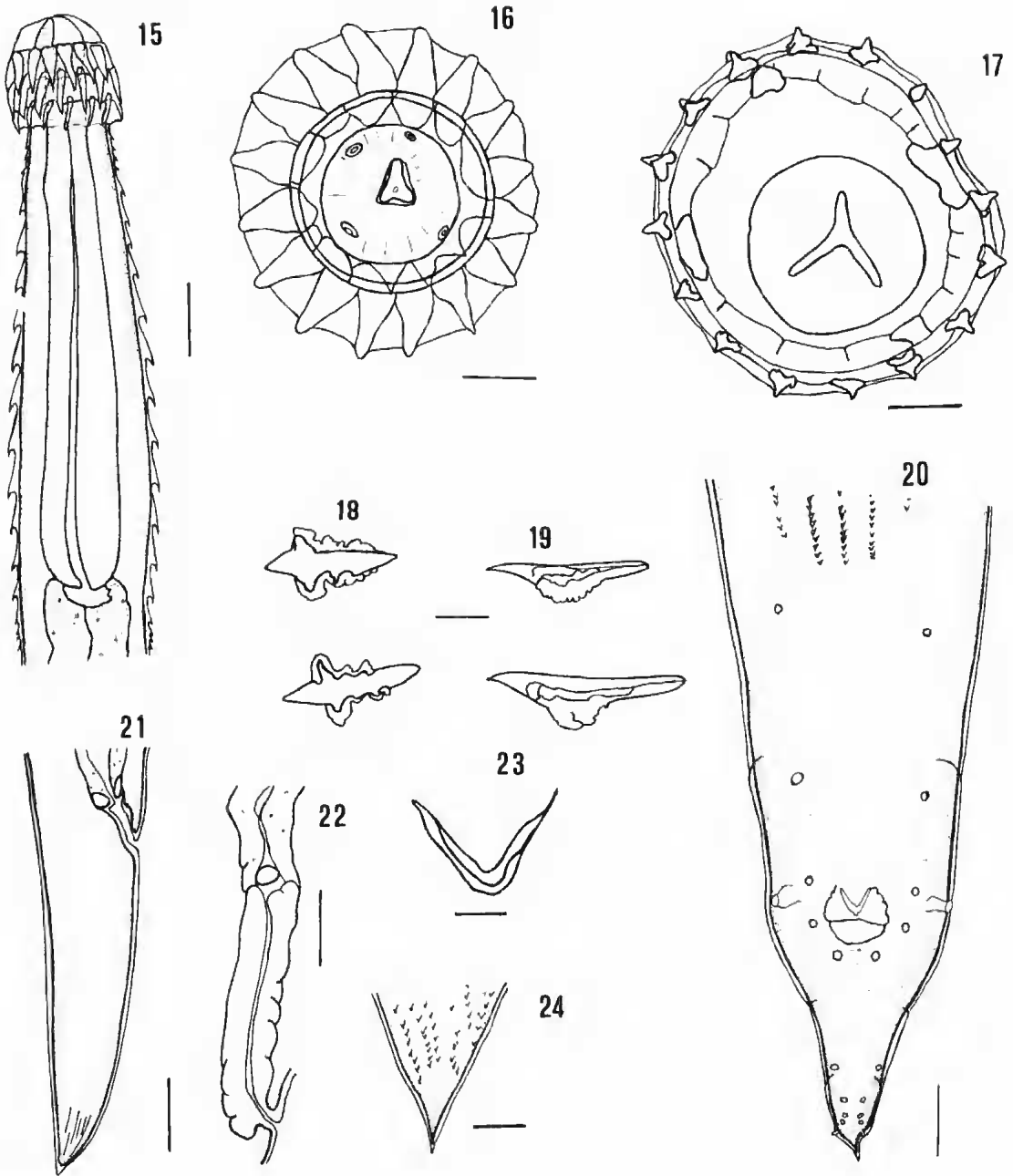
From *Isodon auratus*: 1♂, 1♀, no collection data, AHC 30319.

From *Isodon macrourus* Queensland: 1♂, 1♀, Rollingsstone, (19° 03'S, 146° 24'E), 24.i.1915, BM (NH) 1950: 12.6.165-166; Mossman to Daintree Road, (16° 15'S, 145° 19'E), 2.xi.1991, AHC 30275: 221♂♂, 269♀♀, Mossman, (16° 28'S, 142° 23'E), 17.ii.1958, 5.ii.1958, 4.iii.1958, 12.viii.1958, 12.ii.1958, 20.ii.1958, 9.ii.1958, QM GL14351, GL14361, GL14363, GL14364, GL14365, GL14366, GL14370, GL14372, GL14373, GL14377, GL14381, GL14383; 2♂♂, 4♀♀, Cairns to Mossman Road, (16° 55'S, 145° 46'E), 2.xi.1991, AHC 30274; 2♂♂, Gillies Highway near Lake Barrine, (17° 15'S, 145° 38'E), 29.x.1991, AHC 30279; 6♂♂, 11♀♀, Atherton, (17° 16'S, 145° 29'E), 25.v.1982, CSIRO N1610; 8♂♂, 11♀♀, Yungaburra to Atherton Road, (17° 16'S, 145° 35'E), 29.x.1991, AHC 30278; 7♂♂, 11♀♀, Miriwinji, (17° 24'S, 145° 55'E), 25.ix.1957, QM GL14368; 181♂♂, 189♀♀, Daradgee (17° 29'S 146° 00'E), 20.ii.1959, QM GL12653, GL14367;

8♂♂, 7♀♀, Millaa Millaa to Innisfail Road, (17° 31'S, 145° 37'E), 31.x.1991, AHC 30276; 76♂♂, 133♀♀, Innisfail, (17° 32'S, 146° 01'E), 16.vi.1959, 5.x.1953, 20.vii.1956, 27.vii.1956, 6.vii.1956, 19.vi.1957, 18.ii.1960, AHC 4528, QM GL14357, GL14360, GL14376, GL14378, GL14379, GL14382; 7♂♂, 3♀♀, Atherton to Ravenshoe Road, (17° 36'S, 145° 29'E), 31.x.1991, AHC 30277; 1♂, 4♀♀, Ingham, (18° 39'S, 146° 10'E), 31.x.1991, AHC 30280; 2♂♂, 6♀♀, Palmerston Highway, 29.v.1959, QM GL 14369; 7♀♀, 60km south of Proserpine, (20° 14'S, 152° 35'E) AHC 30266; 3♀♀, Rockhampton to Yeppoon Road, (23° 08'S, 150° 44'E), 16.viii.1990, 3.vii.1992, AHC 30271, 30267; 3♀♀, Yeppoon to Emu Park Road, (23° 10'S, 150° 46'E), 16.ix.1990, AHC 30270; 4♂♂, 15♀♀, Rockhampton to Emu Park Road, (23° 13'S, 150° 50'E) 17.iii.1992, AHC 30272; 1♂, 2♀♀, Rockhampton to Keppel Sands Road, (23° 20'S, 150° 48'E), 18.vii.1992, AHC 30268; 6♀♀, Mt Glorious, (27° 21'S, 152° 54'E) 27.x.1955, QM GL14359; 69♂♂, 120♀♀, Ashgrove, (27° 27'S, 153° 02'E), 27.i.1956, QM GL14347; 120♂♂, 203♀♀, Paddington, Brisbane, (27° 28'S, 153° 01'E), 25.viii.1955, 21.x.1955, 14.ix.1955, AHC 4371, QM GL14350, GL14371; 29♂♂, 55♀♀, Brisbane, (27° 28'S, 153° 01'E), 28.ix.1954, QM GL14340, GL14380; 7♂♂, 18♀♀, Moggill, (27° 29'S, 152° 54'E), 12.x.1967, CSIRO N157; 2♂♂, 2♀♀, Mt Nebo, (27° 33'S, 152° 57'E), 1.x.1954, 23.viii.1993, QM GL14359, AHC 30317, 30818; 8♂♂, 13♀♀, Brookfield, (27° 30'S, 152° 55'E), 20.v.1973, 19.v.1967, AHC 19367, CSIRO N151; 13♂♂, 21♀♀, Rocklea Crossing, 19.v.1967, CSIRO N152; New South Wales: 1♀, no other data, AHC 4462; No locality given: 97♂♂, 171♀♀, 8.iii.1938, 29.ix.1954, 15.x.1954, 28.ix.1954, 22.ii.1956, 12.iii.1958, QM GL14345, GL14346, GL14352, GL14353, GL14354, GL14355, GL14362.

From *Isodon obesulus* New South Wales: 1♂, Sidlings Swamp North, Timbillica State Forest, (37° 17'S, 149° 45'E), 20.vii.1994, CSIRO N4228, Victoria: 11♂♂, 10♀♀, no collection data, AHC 4461, AHC 30297; 6♂♂, 3♀♀, Halls Gap (37° 08'S, 142° 31'E), no date, AHC 30297; 3♂♂, 3♀♀, Mourn Reservoir Grampians, (37° 14'S, 142° 30'E), no date, AHC 30299, South Australia: 3♀♀, Myponga, (35° 23'S, 138° 28'E), no date, AHC 4446; 3♀♀, 1 anterior end, Waitpinga, (35° 36'S, 138° 32'E), no date, AHC 4460; Kangaroo Island, South Australia: 9♀♀, 1♂, Vivonne Bay, (25° 59'S, 137° 13'E), 1.v.1988, AHC 30302; 16♂♂, 39♀♀, Pardana, (35° 47'S, 137° 16'E), 3.xi.1986, AHC 30307; 16♂♂, 28♀♀, Binnowie, (37° 47'S, 136° 59'E), 5.viii.1987, AHC 30303.

From *Perameles nasuta* Queensland: 1♂, 3♀♀, Marceba, (17° 00'S, 145° 26'E), 29.x.1991, AHC 30036.



Figs 15-24. *Linstowinema warringtoni* sp. nov. 15. Anterior end, (lateral view). 16. Cephalic end female, optical section at level of first row of cephalic hooks (*en face* view). 17. Female, hand cut transverse section through body hooks on cuticular dilation. 18. Body hooks (dorsal view). 19. Body hooks (lateral view). 20. Male tail (ventral view). 21. Female tail (lateral view). 22. Vagina (lateral view). 23. Gubernaculum (ventral view). 24. Female tail tip (lateral view). Scale bars = 200 μ m 15, 21; 100 μ m 16, 17, 18, 19, 20, 22, 24; 50 μ m 23.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) files of hooks (Fig. 16), 2nd row longest, 3rd row shortest; neck with 3-7 rows tiny spines; cuticular dilation of oesophageal region bearing 9-13 rows of 14 (male) or 16 (female) files of body hooks (Fig. 17), 1st and last rows smallest, 6th - 8th rows largest, roots of hooks with undulating edges (Figs 18, 19); remainder of body with up to 48 (male) or 54 (female) small spines at each annulation, over whole body of female; extending over $\frac{1}{3}$ of dorsal surface, terminating about 500, anterior to cloaca, not reaching level of most anterior pair of caudal papillae, on ventral surface of male body (Fig. 20). Oesophagus, $\frac{1}{10}$ - $\frac{1}{16}$ body length, simple, club-shaped; terminating at level of 9th-13th row of body hooks (Fig. 15) near posterior end of anterior cuticular dilation. Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male: Length 15-20 (17.5) mm, width 450-750 (565). Cephalic bulb 270-340 (295) long by 270-320 (295) wide; cephalic hooks 1st row 140-170 (155), 2nd row 160-190 (175), 3rd row 100-130 (110) long. Oesophagus 1575-1925 (1743) long, cuticular dilation bearing 9-11 rows of body hooks, deirids 490-550 (530); secretory-excretory pore 360 (n=1); nerve ring 310 (n=1) from anterior end. Spicules similar, equal, without alae, 690-1090 (850) long, about $\frac{1}{10}$ body length. Gubernaculum short, simple, sub-triangular, 50-75 (n=5) long (Fig. 23). Ten pairs caudal papillae; 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively, 1 pair lateral ad-cloacal, 2 pairs lateral pre-cloacal, all same size; 4 pairs papillae, pair phasmids posterior to cloaca near tail tip (Fig. 20). Cloacal region with small cuticular bosses, ala-like expansions absent. Tail 330-430 (390) long.

Female: Length 32-41 (38) mm, width 720-990 (840). Cephalic bulb 350-390 (370) long by 350-400 (280) wide; bearing 3 rows of hooks, 1st row 170-200 (185), 2nd row 180-230 (195), 3rd row 120-150 (130) long. Oesophagus 1870-2500 (2280) long, cuticular dilation bearing 11-13 rows of body hooks. Deirids 580-700 (670); secretory-excretory pore 370-400 (390); nerve ring 300-360 (330) from anterior end. Vulva 12.5-15.6 (14.2) mm from anterior end (Fig. 22). Tail 1000-1900 (1265) long (Figs 21, 24). Vagina about 300 long (n=1). Eggs almost spherical 30-44 (38) by 33-52 (40).

Etymology

This species is named after Warrington Yorke who with P. A. Mapleston carried out much of the early work on this genus.

Type locality

Townsville, Queensland, Australia

Type host

Isodon macrourus (Gould, 1842)

Site in host

Small intestine

Type specimen

Neotype BM (NM) 1950. 12.6. 165-

Remarks

The two worms, 1♂, 1♀, BM (NH) 1950. 12.6.165-166 from *Perameles obesula* collected by Nicoll in 1915 in Queensland are the only specimens registered in Australian or United Kingdom parasite collections which could be the material described by Yorke & Mapleston (1926). On examination these worms were found to have the 11 (male) and 13 (female) body hooks described by Yorke & Mapleston (1926) for *Echinomema cinctum* and to have the "long" oesophagus and all the other characters attributed to *E. cinctum* by Chabaud *et al.* (1980). I therefore designate the male specimen of BM (NH) 1950. 12.6.165-166 as the neotype.

All the specimens identified in this study as *L. warringtoni* conformed to the description given by Chabaud *et al.* (1980) of *L. cinctum*. *Linstowinema warringtoni* sp. nov. differs from all other species in the genus in having up to 9-11 rows of hooks (male) or 11-13 (female) on the oesophageal cuticular dilation and a "long" oesophagus, that is, the oesophagus terminates at or near the final row of body hooks. Male *L. warringtoni* can be distinguished from *L. cinctum* by the combination of characters at the posterior end, i.e., the terminating ventral body spines do not extend to the most anterior pair of papillae in *L. warringtoni* but do in *L. cinctum*, the distance between spines and cloaca is 500 µm not 400 as in *L. cinctum*, the limited extent of cuticular bosses surrounding the cloaca in *L. warringtoni* compared with *L. cinctum*, *L. warringtoni* does not have an ala-like expansion surrounding the cloaca but *L. cinctum* does, and four pairs of papillae not three on the tail tip. The spicules of *L. warringtoni* $\frac{1}{10}$ body length are shorter than those of *L. cinctum* $\frac{1}{10}$ body length. The eggs of *L. warringtoni* are almost spherical but those of *L. cinctum* are ovoid.

Chabaud *et al.* (1980) in their description of *E. cinctum* (*sic*) indicated that they had studied numerous specimens from a range of localities including Woolwonga and Darwin in the Northern Territory. A re-examination of the material from the Northern Territory has shown that it represents a new

species of *Linstowinema*, *L. latens*, described below. The measurements and figures of specimens reported by Chabaud *et al.* (1980) however, are congruent with *L. warringtoni* rather than those of *L. latens*.

Spratt *et al.* (1991) noted that there were no records of helminth parasites from *I. auratus* the golden bandicoot. The finding of *L. warringtoni* in one of five golden bandicoots dissected for this study is therefore the first record of a helminth from this host.

Material registered in the QM as GL14345, 14346, 14352, 14353, 14354, 14355, 14362 was collected by Dr M. J. Mackerras. Therefore although no locality was given these specimens are probably from Queensland.

The finding of *L. warringtoni* in *I. obesulus* is also a new host record. The specimens from Waitpinga, Myponga, Timbillica State Forest and in two of the hosts from Kangaroo Island were found in mixed infections with *L. cinctum*. The geographic distribution of *L. warringtoni* therefore has been shown, in this study, to extend from northern Queensland down the east coast of New South Wales to Victoria, South Australia and offshore to Kangaroo Island. A larger number of *I. obesulus* from the southern states needs to be examined before geographic distributions can be fully mapped. Populations of bandicoots in NSW, Vic. and SA, now have patchy distributions over a reduced range (Braithwaite 1995) and attempts to collect additional specimens of *I. obesulus* for parasitological examination have been unsuccessful to date. Further work on the southern geographic distribution of *L. warringtoni* will be problematic, as bandicoots become more difficult to collect.

The specimens of *L. warringtoni* found in a single *P. nasuta* suggest either a natural low prevalence of infection, or an occasional, incidental infection of this host.

Linstowinema latens sp.nov.
(FIGS 25-36)

Synonym: *Echinonema cinctum sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980: pp. 435-436 (in part); *sensu* Spratt, Beveridge & Walter, 1991: p. 25 (in part).

Material examined

Type material: Holotype ♂, allotype ♀, from *Isodon macrourus*, Walsh Point, (15° 08'S, 125° 46'E), Mitchell Plateau, Western Australia, 22.vii.1982; AHC 30322, 30323, 43♂♂, 65♀♀, paratypes AHC 13028, WAM 110-83, 116-83.

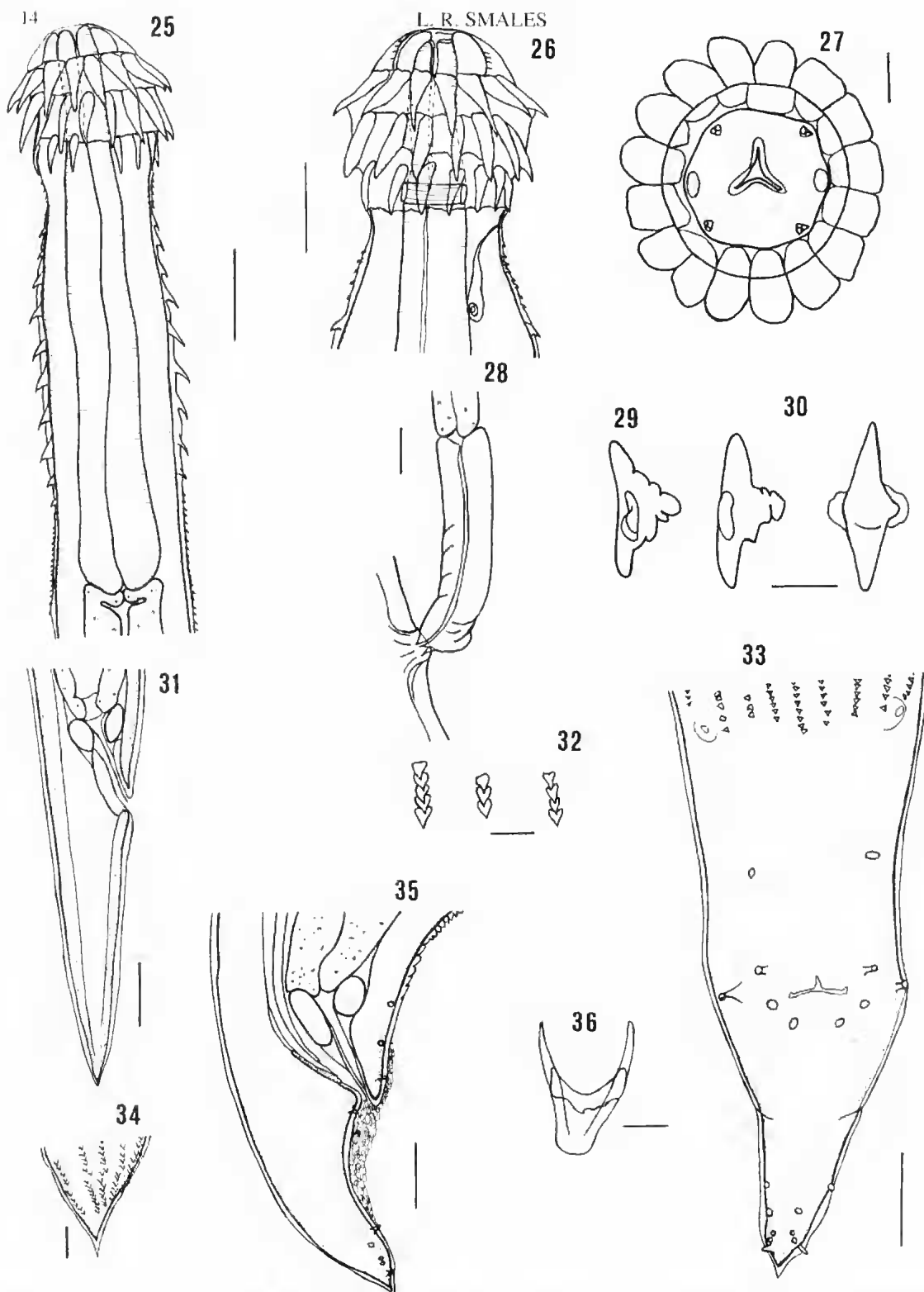
Other material: From *Isodon macrourus* Western Australia: 1♂, 4♀♀, Mt Hart, Kimberley Ranges,

(16° 48'S, 124° 55'E), 22.x.1993, 24.x.1993, AHC 30289, 30290. Northern Territory: 16♂♂, 18♀♀, Darwin, (12° 27'S, 130° 50'E), no date, 19.vi.1993, 27.vi.1995, 28.vi.1995, AHC 4703, 30287, CSIRO N4413, N4414; 7♂♂, 7♀♀, near Byers Rd, Stuart Highway turnoff, (12° 30'S, 130° 50'E), 18.vi.1993, AHC 30284, 30285; 7♂♂, 10♀♀, Adelaide River, Arnhem Highway, (12° 28'S, 131° 14'E), 20.vi.1993, AHC 30288; 13♂♂, 12♀♀, Bees Creek, off Stuart Highway, (12° 35'S, 131° 04'E), 17.vi.1993, AHC 30286; 11♂♂, 8♀♀, Jabiluka, August 1979, AHC 6421; 3♀♀, Woolwonga, (12° 45'S, 132° 39'E), 19.x.1972, CSIRO N159. Queensland: 6♂♂, 11♀♀, Atherton (17° 15'S, 145° 29'E), 25.v.1928, CSIRO N1610; 11♂♂, 14♀♀, 14km north of Atherton (17° 15'S 145° 29'E), 15.iii.1982, N1532; 19♂♂, 12♀♀, Yungaburra to Atherton Rd, (17° 15'S 145° 30'E), 29.x.1991, 1.xi.1991, AHC 30278, 30281; 1♂, Gillies Highway near Lake Barrine (17° 16'S, 145° 35'E), 29.x.1991, AHC 30279; 6♂♂, 8♀♀, Gillies Highway near Yungaburra, (17° 16'S, 145° 35'E), 29.x.1991, AHC 30283; 23♂♂, 116♀♀, Mareeba to Kuranda Rd (17° 00'S, 145° 26'E), 2.xi.1991, AHC 30282.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) files of hooks, 2nd row longest, 3rd row shortest (Figs 26, 27); neck with 2-9 rows tiny spines; cuticular dilation of oesophageal region bearing 14 (male) or 16 (female) files of body hooks, first and last rows very small, 6th - 7th rows largest; roots of hooks without undulating edges (Figs 29, 30); remainder of body with up to 44 (male) or 60 (female) small spines at each annulation, over whole body of female; extending over $\frac{9}{10}$ of dorsal body surface, terminating about 300-400 anterior to cloaca, level with anterior pair of caudal papillae, on ventral surface of male body (Figs 32, 33). Oesophagus $\frac{1}{10}$ - $\frac{1}{11}$ (male) $\frac{1}{15}$ - $\frac{1}{16}$ (female) body length, simple, club-shaped, terminating posterior to the oesophageal cuticular dilation (Fig. 25). Nerve ring surrounding oesophagus within cephalic bulb, secretory-excretory pore in neck, deirids conical, at level of first row of body hooks.

Male: (measurements of specimens from Western Australia, followed by measurements of specimens from Northern Territory). Length 15-18 (16), 15-21 (18.5) mm, width 425-625 (490), 515-715 (600). Cephalic bulb 280-350 (325) long by 280-380 (340) wide, 275-435 (350) long by 290-385 (340) wide; cephalic hooks, 1st row 150-180 (152), 105-165 (140), 2nd row 160-190 (168), 125-195 (155), 3rd row 100-110 (108), 72-117 (94) long (Fig. 26). Oesophagus 1200-1825 (1555), 1325-1990 (1715) long, cuticular dilation bearing 8-10 rows body hooks. Deirids 540-690 (610), 390-650 (530);



Figs 25-36. *Linstowinema latens* sp. nov. 25. Anterior end, (lateral view). 26. Cephalic bulb (lateral view). 27. Cephalic end female, optical section at level of first row of hooks (*en face* view). 28. Vagina (lateral view). 29. Body hooks (lateral view). 30. Body hook (dorsal view). 31. Female tail (lateral view). 32. Male posterior body spines (ventral view). 33. Male tail (ventral view). 34. Female tail tip (lateral view). 35. Male tail (lateral view). 36. Gubernaculum (ventral view). Scale bars = 200 μ m 25, 26; 50 μ m 27; 100 μ m 28, 31, 33, 35; 25 μ m 29, 30, 32, 34, 36.

secretory-excretory pore not seen, 230-495 (365); nerve ring 300 (n=1), 225-365 (275) from anterior end; Spicules equal similar, without alae, 830-1090 (995), 830-1100 (1005) long, about $\frac{1}{10}$ to $\frac{1}{8}$ body length. Gubernaculum short, simple, sub-triangular, 61-68 (n=3), 66-79 (n=5) long (Fig. 36). 10 pairs caudal papillae; 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively, 1 pair lateral ad-cloacal 2 pairs lateral pre-cloacal, all same size; 4 pairs papillae, pair phasmids, ala-like expansions absent posterior to cloaca, near tail tip (Fig. 33). Cloacal region with small cuticular bosses, ala-like expansions absent. Tail 250-340 (310), 255-320 (305) long (Fig. 35).

Female: Length 20-38 (30), 25-41 (30) mm, width 420-750 (590), 665-1175 (840). Cephalic bulb 300-380 (350), 230-510 (385) long by 350-500 (385), 375-530 (430) wide; bearing 3 rows of hooks, 1st row 160-190 (175), 135-190 (155), 2nd row 170-190 (180), 140-195 (170), 3rd row 100-120 (110), 90-135 (110) long. Oesophagus 1450-2075 (1790), 1565-2430 (1970) long; cuticular dilation bearing 9-12 body hooks. Deirids 600-700 (660), 325-770 (495); secretory-excretory pore not seen, 295-590 (420); nerve ring not seen, 205-405 (355) (n=5) from anterior end (Fig. 28). Vulva 9.2-14.7 (11.8), 9.2-17.2 (11.9) mm from anterior end. Vagina about 115 (n=2). Eggs almost spherical 36-60 (50), 33-42 (35) by 33-39 (34). Tail 790-1210 (980), 920-1615 (1160) long (Figs 31, 34).

Etymology

The species name is derived from the Latin *latens* meaning hidden, since it was not found when the material was first examined.

Type host

Isodon macrourus (Gould, 1842)

Type locality

Mitchell Plateau, Western Australia, Australia.

Site in host

Small intestine

Type specimens

Holotype male, AHC 30322, allotype female, AHC 30323, paratypes AHC 13028

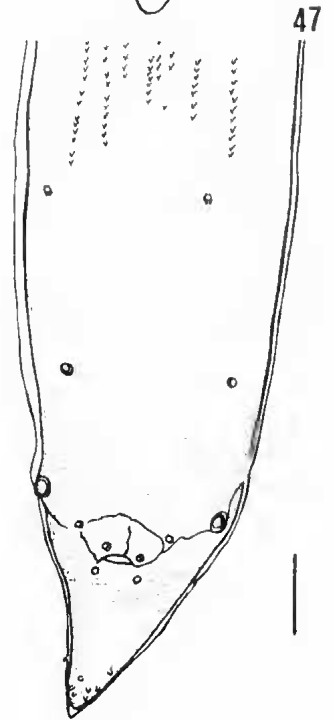
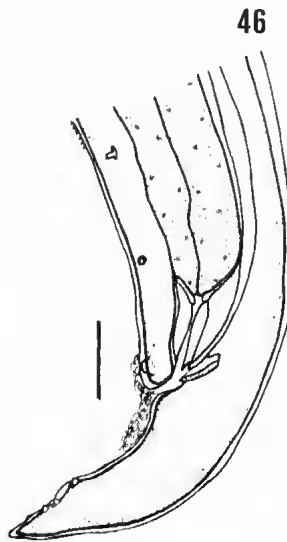
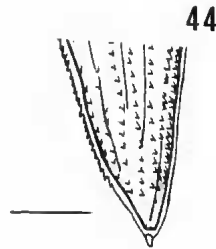
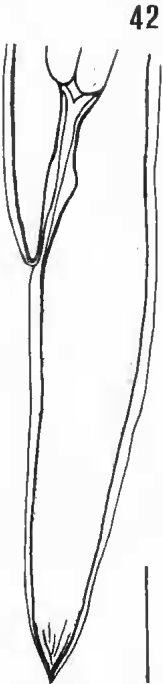
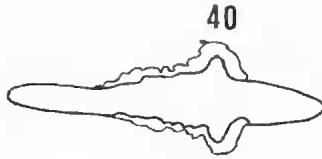
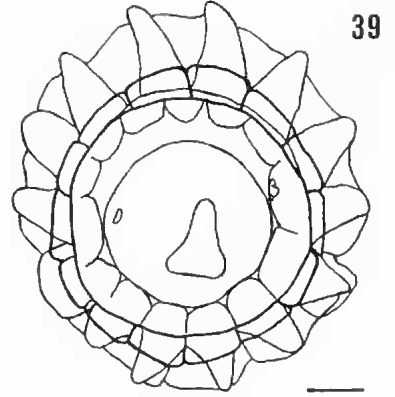
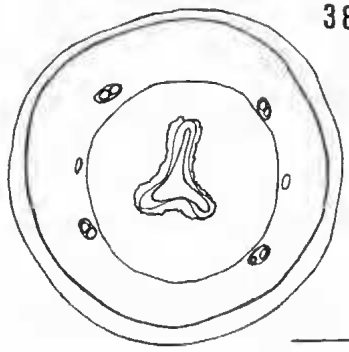
Remarks

Linstowinema latens sp. nov. resembles *L. warringtoni*, also occurring in *I. macrourus*, in being of similar size, (males 15-21 mm in *L. latens* compared with 15-20 mm long in *L. warringtoni*),

having the oesophagus of similar length (1575-1925 in *L. latens* compared with 1200-1825 in *L. warringtoni* males) and four pairs of papillae on the male tail. The oesophagus in *L. latens*, however, terminates posteriorly to the hooks surrounding the oesophageal region whereas that of *L. warringtoni* terminates at about the level of the 9th-13th row of hooks. *L. latens* has 8-10 (male) or 9-12 (female) rows of hooks, roots without undulating edges, while *L. warringtoni* has 9-11 (male) or 11-13 (female) rows of hooks, with roots having undulating edges on the dilated cuticular region. The body spines on the dorsal surface of male *L. latens* extend further towards the posterior end, (about $\frac{9}{10}$ of the body), than on *L. warringtoni* (about $\frac{4}{5}$ of the body). Ventrally the body spines extend to the same level as the most anterior pair of caudal papillae on *L. latens*, but do not on *L. warringtoni*. The male tail is longer in *L. warringtoni* (330-430) than in *L. latens* (250-340). The vagina of *L. latens* (115) is shorter than that of *L. warringtoni* (300).

Specimens were found in *I. macrourus* from northern Western Australia, the Northern Territory and northern Queensland. The population of northern brown bandicoots in Western Australia is isolated from that of the Northern Territory and Queensland (Gordon 1995), but measurements of worms from hosts occurring in the Kimberley, Western Australia, are consistent with those from Darwin, Northern Territory. The only morphological difference observed between these populations was that the first row of cephalic hooks of the Kimberley specimens was almost as long as the second row, 150-180, compared with 160-196 in males, but in the Darwin specimens the difference in length between the two rows of hooks was more marked, 105-163, compared with 126-195. This difference is not considered to be significant and as the Queensland worms were similar to those from the Northern Territory, the material from all three localities is considered to be conspecific.

The northern brown bandicoots collected from northern Queensland were infected with *L. warringtoni*, 8 hosts, *L. latens*, 4 hosts, or both species, 3 hosts. Chabaud *et al.* (1980) identified all the material they examined from the Northern Territory and northern Queensland as *L. cinetum*, now *L. warringtoni*. It is not possible to determine from their paper which, if any, specimens from northern Queensland, presently lodged in the QM, SAMA or CSIRO collections, they examined. The specimens they examined from Woolyonga and Darwin in the Northern Territory have been re-examined for this study, and are all *latens*. The Queensland material examined by Chabaud *et al.* (1980) could have been either *L. warringtoni*, *L. latens*, or both.



Linstowinema inglisi (Chabaud, Seureau, Beveridge, Bañ & Durette-Desset, 1980)
comb. nov.
(FIGS 37-47)

Synonymy: *Echinonema cinetum* sensu Inglis, 1967: pp. 122, 128, 131-133, Figs 8-10, *Echinonema inglisi* Chabaud, Seureau, Beveridge, Bañ & Durette-Desset, 1980: pp. 437-438; Spratt, Beveridge & Walter, 1991: p. 26.

Material examined

From *Isodon obesulus* Western Australia: 4 ♂♂, 3 ♀♀, Murdoch, (31° 57'S, 115° 51'E), 27.v.1981, AHC 8901; 40 ♂♂, 106 ♀♀, Perth, (31° 57', 115° 51'E), Jan. 1993, 9.i.1993, 5.ii.1993, 1993, AHC 30257, 30258, 30259, 30260, 30262, 30263, 30264, 30265; 11 ♂♂, 44 ♀♀, Wattle Grove (32° 02'S, 116° 00'E), 5.v.1966, BM (NH) 1967, 616-626, WAM 25-70; 10 ♂♂, 10 ♀♀, Glen Forest, 10.viii.66, AHC 29760; BM (NH) 1967, 473-523; 4 ♂♂, 10 ♀♀, Forestdale, 15.xii.1978, AHC 8885; 40 ♂♂, 10 ♀♀, Jarrahdale, (32° 30'S, 16° 07'E), 28.x.1993, AHC 30261; 4 ♂♂, 8 ♀♀, Albany, (35° 00'S, 117° 52'E), 18.xi.1994, 19.xi.1994, CSIRO N4242, N4243; 19 ♂♂, 32 ♀♀, Manjimup, (35° 15'S, 116° 09'E), 27.vi.1993, 16.ix.1993, AHC 30255, 30256; 62 ♂♂, 155 ♀♀, no locality given, 22.x.1977, AHC 8888.

Description

Cephalic bulb with 3 rows of 14 (male) (Figs 38, 39) or 16 (female) files of hooks 2nd row longest, 3rd row shortest; neck with 5-11 rows tiny spines; cuticular dilation of oesophageal region bearing 10-14 rows, 14 (male) or 16 (female) files of body hooks, 1st and last rows smallest, 7th - 9th rows hooks largest (Figs 3, 7); roots of hooks with undulating edges (Figs 40, 41). Remainder of body with up to 35 (male), or 45 (female) small spines at each annulation, over whole body of female, extending to 400 µm from tail tip on dorsal surface and about 300-500 anterior to cloaca, not extending to anterior pair of caudal papillae, on ventral surface of male body (Fig. 47). Oesophagus $1/11$ (male) to $1/14$ (female) body length, simple, club-shaped, terminating level with 8th-9th row of hooks. Nerve ring surrounding oesophagus within cephalic bulb, secretory-excretory pore in neck, deirids conical, at level of 1st row of body hooks.

Male: Length 11-18 (15) mm, width 325-625 (540). Cephalic bulb 266-325 (272) long by 247-350 (309) wide; cephalic hooks, 1st row 140-180 (155), 2nd row 160-200 (180), 3rd row 115-140 (125) long (Figs 3, 7). Oesophagus 1120-1565 (1400) long; cuticular dilation bearing 10-12 rows body hooks, Deirids 410-650 (520); secretory-excretory pore not seen; nerve ring 312 ($n=1$) from anterior end. Spicules similar, equal, without alae 700-1200 (985) long, about $1/12$ body length. Gubernaculum short, sub-triangular, 50-58 ($n=5$) long (Fig. 45). Nine pairs caudal papillae: 3 pairs ventral and immediately pre-, ad- and post-cloacal; 1 large pair lateral, ad-cloacal, 2 pairs lateral, pre-cloacal, 3 pairs papillae, pair phasmids well posterior to cloaca, near tail tip (Fig. 47). Cloacal region with small cuticular bosses, ala-like extensions of body absent. Tail 150-350 (265) long (Fig. 46).

Female: Length 15-30 (24) mm, width 560-935 (700). Cephalic bulb 312-357 (334) long by 293-422 (334) wide; cephalic hooks, 1st row 155-195 (180), 2nd row 180-235 (205), 3rd row 115-150 (125) long. Oesophagus 1385-1835 (1655) long; cuticular dilation bearing 12-14 rows body hooks, Deirids 485-570 (545); secretory-excretory pore 390 ($n=1$) from anterior end; nerve ring not seen. Vulva 9.8-10.2 mm ($n=2$) (Fig. 43) from anterior end. Vagina about 350 ($n=1$). Eggs almost spherical 40-48 (44) by 36-45 (40). Tail 610-920 (730) long (Figs 42, 44).

Type host

Isodon obesulus (Shaw, 1797)

Type locality

Wattle Grove, near Perth, Western Australia, Australia

Site in host

Small intestine

Type specimen

Neotype BM(NH) 1967 616

Remarks

Material from *I. obesulus* from Wattle Grove, collected on 5.v.1966 and identified by Inglis is

Figs 37-47. *Linstowinema inglisi* (Chabaud, Seureau, Beveridge, Bañ & Durette-Desset, 1980). 37. Anterior end, (lateral view). 38. Cephalic end (*en face* view). 39. Cephalic end male, optical section at level of first row of hooks (*en face* view). 40. Body hook (dorsal view). 41. Body hook (lateral view). 42. Female tail (lateral view). 43. Vagina (lateral view). 44. Female tail tip (lateral view). 45. Gubernaculum (ventral view). 46. Male tail (lateral view). 47. Male tail (ventral view). Scale bars = 200 µm 37, 42; 50 µm 38, 39, 43, 44; 100 µm 40, 41, 46, 47; 25 µm 45.

deposited in the WAM and BM (NH). This appears to be the material described as *E. cinctum* by Inglis (1967). I therefore designate a specimen from BM (NH) 1967. 616-626 as the neotype.

Linstowinema inglisi (Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980) can be distinguished from *L. warringtoni* and *L. latens* in having the oesophagus terminating within the anterior cuticular dilation. *Linstowinema inglisi* has 10-12 (male) and 12-14 (female) rows of body hooks compared with 9-11 and 11-13 rows for *L. warringtoni* and 8-10 and 9-12 rows for *L. latens*. The spicules of *L. inglisi* ($1/15$ body length) are relatively longer than for *L. warringtoni* ($1/20$ body length) and *L. latens* ($1/17$ body length). The male tail of *L. inglisi* also differs from both *L. warringtoni* and *L. latens* in being shorter (150-350 (265) compared with 330-430 (390) and 250-340 (307) respectively and in having only 3 pairs of papillae rather than 4. The female tail is also shorter (610-920 (730)) in *L. inglisi* compared with *L. warringtoni* and *L. latens* (1000-1900 (1265)) and 790-1615 (1070), respectively.

The pair of lateral papillae level with the cloacal opening is more prominent than the other pairs of papillae surrounding and anterior to the cloaca of *L. inglisi*. In this respect, *L. inglisi* resembles *L. edmondsi* from dasyurid marsupials but *L. inglisi* differs from *L. edmondsi* in having the 2nd, not the 1st row of cephalic hooks the longest. *Linstowinema edmondsi* occurs in *Dasyurus hallucatus* from the Northern Territory while *L. inglisi* occurs in *I. obesulus* from southern Western Australia.

Linstowinema inglisi can be distinguished from *L. cinctum*, which also occurs in *I. obesulus* and has the oesophagus terminating within the cuticular dilation of the oesophageal region at about the 9th row of hooks, by the number of rows of body hooks, 10-12 (male) and 12-14 (female) compared with 13-16 and 14-18 in *L. cinctum*. The differences between *L. cinctum* and *L. inglisi* are discussed in detail under *L. cinctum*.

The measurements of *L. inglisi* from this study are congruent with those given by Inglis (1967). Any differences between the two sets of measurements are because Inglis (1967) measured smaller worms, 3.29-11.39 for the males compared with 11-18 in this study and 10.1-18.4 for the females compared with 15-30 in this study. Chabaud *et al.* (1980) described

L. inglisi males as having spines covering only $1/3$ of the body dorsally. A careful examination of specimens for this study, however, has shown that the dorsal spines, although tiny, extend along about $2/3$ of body, that is, further towards the tail tip than do the ventral spines.

Linstowinema inglisi has been found only in *I. obesulus* from the south of Western Australia.

Linstowinema tasmaniense sp. nov.

(FIGS 48-61)

Synonyms: *Echinonema cinctum sensu* Munday & Green, 1972: p. 10 (in part), *Echinonema uglii sensu* Spratt, Beveridge & Walter, 1991: p. 26 (in part), *Echinonema* sp.1 Chabaud, Seureau, Beveridge, Bain & Durette-Desset 1980: p. 453; Spratt, Beveridge & Walter, 1991: p. 26.

Material examined

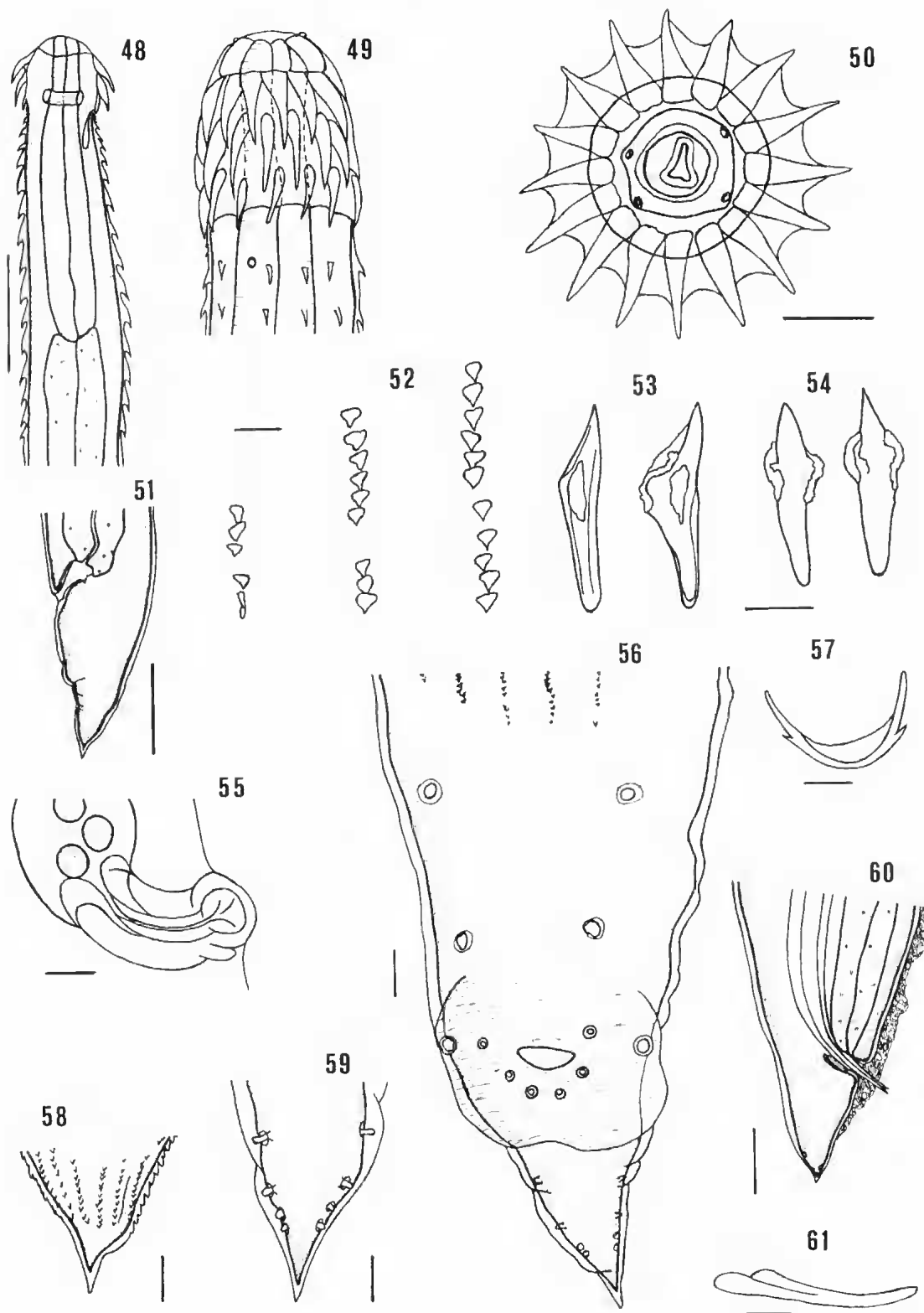
Type material: Holotype ♂, allotype ♀, from *Isodon obesulus*, Kingston (42° 59'S, 147° 18'E), Tasmania, 11.vii.1992, AHC 30320, 30321. Paratypes 12♂♂, 11♀♀, AHC 30310, 30311.

Other material: From *Isodon obesulus* South Australia, Kangaroo Island: 12♂♂, 4♀♀, Vivonne Bay, (35° 59'S, 137° 13'E), no date, l.v.1988, AHC 4458, 30302; 13♂♂, 24♀♀, Hundred of Gosse, June 1983, AHC 30305; 8♂♂, 17♀♀, Karatta, (35° 59'S, 136° 56'E), Sept. 1983, AHC 30306; 13♂♂, 15♀♀, Pandana, (35° 47'S, 137° 16'E), 12.iv.1991, 3.xi.1986, AHC 30300, 30307; 1♂, 1♀, Seal Bay, (36° 00'S, 137° 20'E), 4.i.1987, AHC 30304. Tasmania: 5♂♂, 15♀♀, Beaconsfield, (41° 12'S, 146° 49'E), 1991, AHC 30315; 3♂♂, Glengarry, (41° 21'S, 146° 52'E), 1992, AHC 30309; 1♀, Hobart, (42° 53'S, 147° 19'E), 25.vi.1982, CSIRO N1674; 7♂♂, 8♀♀, Gog Range, (42° 59'S, 147° 18'E), 8.vii.1992, AHC 30308; 8♂♂, 13♀♀, Margate tip, (43° 02'S, 147° 16'E), 10.iii.1993, AHC 30312; 1♂, Upper Dromedary, no date given, AHC 4530; 12♂♂, 19♀♀, no collection data, AHC 30313, 30314.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) (Figs 49, 50) files of hooks. 2nd row longest, 3rd row shortest (Fig. 49); neck with 5-8 rows tiny

Figs 48-61. *Linstowinema tasmaniense* sp. nov. 48. Anterior end, optical section (lateral view). 49. Cephalic bulb (lateral view). 50. Cephalic end female, optical section at level of first row of hooks (*en face* view). 51. Female tail (lateral view). 52. Male posterior body spines (ventral view). 53. Body hooks (lateral view). 54. Body hooks (dorsal view). 55. Vagina (lateral view). 56. Male tail (ventral view). 57. Gubernaculum (ventral view). 58. Female tail tip (lateral view). 59. Male tail tip (ventral view). 60. Male tail tip (ventral view). 61. Gubernaculum (lateral view). Scale bars = 500 µm 48, 51; 200 µm 49, 60; 100 µm 50; 50 µm 52, 53, 54, 55, 56; 25 µm 57, 58, 59; 12 µm 61.



spines; cuticular dilation of oesophageal region bearing 13-15 rows of 14 (male) or 16 (female) files of body hooks 1st and last rows smallest, 9th-10th rows largest; roots of hooks without undulating edges (Figs 53, 54); remainder of body with up to 46 (male) or 66 (female) small spines at each annulation, over whole body of female, extending over $2/3$ of dorsal surface, terminating about 350 anterior to cloaca, not reaching level of most anterior pair of caudal papillae, on ventral surface of male body (Fig. 56). Oesophagus about $1/6-1/3$ body length, simple, club-shaped, terminating at level of 8th-10th row of body hooks (Fig. 48). Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male: Length 11-14 (12.6) mm, width 455-715 (605). Cephalic bulb 215-295 (255) long by 270-390 (325) wide; bearing 3 rows of hooks, 1st row 140-195 (170), 2nd row 175-225 (200), 3rd row 105-130 (120) long (Fig. 49). Oesophagus 1105-1580 (1360) long; cuticular dilation bearing 12-13 rows of body hooks; deirids 355-480 (430), secretory-excretory pore 300-440 (365) ($n=6$); nerve ring 240-300 (280) ($n=4$) from anterior end. Spicules similar, equal, without alae 720-1030 (890) long, about $1/14$ body length. Gubernaculum short, simple, subtriangular, 50-55 ($n=3$) long (Figs. 57, 61). Ten pairs caudal papillae: 3 pairs ventral and immediately pre- and post-cloacal respectively, 1 pair lateral ad-cloacal, 2 pairs lateral pre-cloacal (Fig. 56); 3 lateral pairs larger (Fig. 56); 3 pairs papillae, pair phasimids posterior to cloaca, near tail tip (Fig. 59). Cloacal region with small cuticular bosses; ala-like expansion of body surrounding cloaca. Tail 235-325 (285) long (Fig. 60).

Female: Length 19-22 (21) mm, width 815-1155 (965). Cephalic bulb 195-325 (255) long by 370-505 (460) wide; bearing 3 rows of hooks, 1st row 190-210 (205), 2nd row 220-265 (245), 3rd row 125-170 (150) long. Oesophagus 1445-1990 (1615) long; cuticular dilation bearing 14-15 rows body hooks. Deirids 355-450 (405); secretory-excretory pore 375 ($n=1$) from anterior end; nerve ring not seen. Vulva 5525-7600 (6500) ($n=3$) long (Fig. 55). Vagina 175 ($n=1$) long. Tail 715-935 (810) long (Figs 51, 58). Eggs almost spherical 36-48 (42) by 33-45 (38).

Remarks

Linstowinema tasmaniense sp. nov. resembles *L. inglisi* and *L. cinctum*, also occurring in *L. obesus* and having three pairs of papillae on the male tail and the oesophagus terminating within the cuticular dilation of the oesophageal region, at about the 8th-11th row of hooks. *Linstowinema tasmaniense* can be differentiated from *L. inglisi* in having 12-13

(male) and 14-15 (female) rows of body hooks without undulating edges, compared with 10-12 (male) and 12-14 (female) rows of body hooks with undulating edges and from *L. cinctum* which has 13-16 (male) and 14-18 (female) rows of body hooks with undulating edges. *Linstowinema tasmaniense* further differs from *L. inglisi* in having all three pairs of papillae lateral and anterior to the cloaca, larger than those surrounding the cloaca, and in having the cloacal region with ala-like extensions of the body. *Linstowinema inglisi* has only one pair of larger lateral ad-cloacal papillae and does not have the ala-like extensions. *Linstowinema cinctum*, which does have ala-like extensions of the body, has ventral body spines extending to the level of the most anterior pair of lateral caudal papillae but *L. tasmaniense* does not. *Linstowinema cinctum* has all six pairs of papillae lateral and anterior to the cloaca the same size but *L. tasmaniense* has the three lateral pairs larger. The gubernaculum is more U-shaped in ventral view in *L. tasmaniense* than in *L. inglisi* or *L. cinctum*. Female *L. tasmaniense* have a shorter tail 715-935 (810) than *L. cinctum* 986-1122 (1050). The oesophagus is about $1/6$ body length in *L. tasmaniense* males compared with $1/8$ in *L. cinctum* and $1/11$ in *L. inglisi*. The vulva is closer to the anterior end in *L. tasmaniense*, about 0.6 mm compared with 1.0 mm in *L. inglisi* and 1.2 mm in *L. cinctum*. The vagina of *L. tasmaniense*, 175, is shorter than in *L. cinctum* 300 and *L. inglisi* 350.

Chabaud *et al.* (1980) figured the tail of a male specimen, registered as AHC 4530, from *L. obesus*, Upper Dromedary, Tasmania. There is now only one damaged male specimen in the bottle available for comparison, but such characters as can be seen, and the drawings of Chabaud *et al.* (1980) (Fig. 5 B, E, p. 438), are consistent with *L. tasmaniense*.

Linstowinema tasmaniense appears to have a geographic range which extends across Tasmania and Kangaroo Island. Three hosts from Kangaroo Island were infected with two species of *Linstowinema*, one with *L. cinctum* and *L. tasmaniense*, and two with *L. warringtoni* and *L. tasmaniense*. This suggests past links between Kangaroo Island hosts, mainland Australian hosts and Tasmanian hosts.

Etymology

The species is named according to a label found in AHC 1820, "*E. cinctum tasmaniensis*", here determined to be *L. cinctum*, which had apparently been written by Chabaud *et al.* when preparing their paper of 1980.

Type locality

Kingston, Tasmania, Australia

*Type host**Isodon obesulus* (Shaw, 1797)*Site in host*

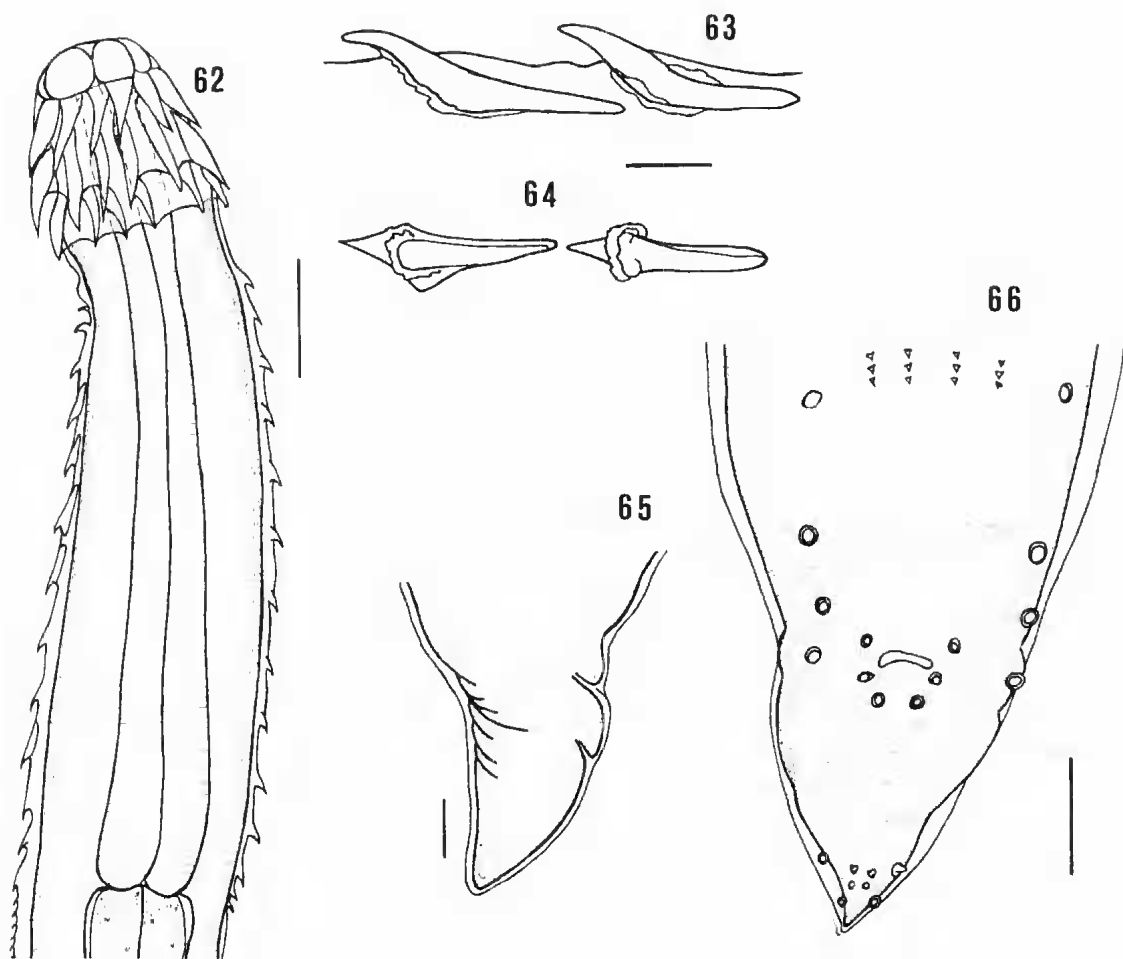
Small intestine

Type specimens

Holotype male, AHC 30320, allotype female, AHC 30321, paratypes AHC 30310

Linstowinema peramelis sp. nov.
(FIGS 62-66)Synonym: *Echinonema cinctum sensu* Spratt,
Beveridge & Walters 1991: p. 22.*Material examined**Type material*: Holotype ♂, AHC 30023, allotype ♀, AHC 30097, from *Perameles bougainville*.*Other material*: From *Perameles bougainville* 1 ♂, 1 ♀, 1 anterior end, 1 posterior end, no collection data, AHC 30055, 30054, 30053; 1 ♂, 1 ♀, 3 anterior ends, 2 posterior ends, no collection data, AHC 4522; 2 ♂♂, 1 ♀, captive, University Adelaide, no date, AHC 13928.*Description*

Cephalic bulb with 3 rows of 15 (male) or 16 (female) files of hooks, 2nd row longest, 3rd row much the smallest (Fig. 62); neck with about 6 rows



Figs 62-66. *Linstowinema peramelis* sp. nov. 62. Anterior end (lateral view). 63. Body hooks (lateral view). 64. Body hooks (dorsal view). 65. Female tail (lateral view). 66. Male tail (ventral view). Scale bars = 200 µm 62; 25 µm 63, 64; 100 µm 65, 66.

tiny spines; cuticular dilation of oesophageal region bearing 10-12 rows, 14 (male) or 16 (female) files of body hooks, first and last rows smallest, 6th-8th rows largest, roots of hooks without undulating edges (Figs 63, 64); remainder of body with a row of small spines at each cuticular annulation (numbers of spines not counted), over whole body of female; extending over $\frac{1}{4}$ dorsal surface, terminating about 300 anterior to cloaca ventrally, reaching level of most anterior pair of caudal papillae, on ventral surface of male body (Fig. 66). Oesophagus simple club-shaped, about $\frac{1}{10}$ body length, terminating at 11th-12th row of hooks (Fig. 62). Secretory-excretory pore, detritus and nerve ring not seen.

Male: (n=2). Length 9, 9 mm, width 475, 475. Cephalic bulb 235, 325 long by 234, 267 wide; cephalic hooks 1st row 123, 129, 2nd row 117, 150, 3rd row 75, 93 long. Oesophagus 795, 970 long, cuticular dilation bearing 11-12 rows body hooks. Spicules similar, equal, without alae, 950, 1050 long, about $\frac{1}{6}$ body length. Cuticular annulation short, simple, sub-triangular, 11 pairs caudal papillae; 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively; 1 pair lateral ad-cloacal, 3 pairs lateral pre-cloacal; 7 anterior pairs all about same size; 3 pairs papillae, pair phasmids well posterior to cloaca, anal tail tip (Fig. 66). Cloacal region with small cuticular bosses, ala-like expansion absent. Tail 210, 240 long.

Female: (n=2) Length 11 mm, width 520. Cephalic hooks 1st row 260, 135, 2nd row 140, 260, 3rd row 78, 140. Oesophagus 1190, 1250 long; cuticular dilation bearing 10-12 rows body hooks. Tail 460 long (Fig. 65). Vulva not seen. Eggs more or less spherical, 51-57 by 60-63.

Remarks

Although there was only a small number of specimens and they were all in poor condition, significant differences between these specimens and other species of *Linstowinema* could be found. Although elements such as the vulva could not be seen, the worms appeared to be mature, having fertilized eggs *in vitro*. Since *P. bougainville* is now extinct on mainland Australia and fully protected on the islands in Shark Bay Western Australia, it is unlikely that any more specimens will become available. Accordingly, this somewhat incomplete description is presented as the best possible of the species under the circumstances. *Linstowinema peramelis* sp. nov. most closely resembles *L. warringtoni* and the species that have been distinguished in the discussion of *L. warringtoni*, in that there are no more than 11-12 (male) and 10-12 (female) rows of body hooks compared with 9-11 (male) and 11-13 (female) and the oesophagus is

relatively long, extending to the 11th or 12th row of body hooks. The two species can be differentiated by size. *Linstowinema warringtoni* males, 15-20 mm, and females, 32-41 mm, are much larger worms than *L. peramelis*, 9 and 11 mm, respectively. *Linstowinema peramelis* has plain edges on the roots of its body hooks but *L. warringtoni* has undulating edges. The numbers and arrangement of papillae on the posterior end of the male are also different. *Linstowinema peramelis* is the only species of *Linstowinema* with four pairs of papillae lateral and anterior to the cloaca; all other species have three. The spicules of *L. peramelis* (950-1050, $\frac{1}{6}$ body length), are relatively longer than those of *L. warringtoni* (690-1090, $\frac{1}{20}$ body length). *Linstowinema peramelis* has three pairs of papillae near the caudal tip but *L. warringtoni* has five. The tail of *L. peramelis* (210, 240 (male), 460 (female)), is shorter than that of *L. warringtoni* (330-430 and 1000-1900). The eggs of *L. peramelis* (51-57 by 60-63) are larger than those of *L. warringtoni* (30-44 by 33-48).

Linstowinema peramelis is similar to *L. inglesi* and *L. cinctum*, in having three pairs of caudal papillae. It can be differentiated from these two species in having a relatively long oesophagus, terminating at the level of the posterior rows of hooks on the cuticular dilation of the oesophageal region, and not within it, and in having up to 12 rows of body hooks without undulating edges compared with *L. melisi*, up to 14, and *L. cinctum*, up to 18 rows of body hooks with undulating edges.

Linstowinema peramelis resembles *L. tasmaniense* in having four pairs of caudal papillae near the caudal tip and body hooks without undulating edges, but differs from *L. tasmaniense* in having the oesophagus terminating at the end of the cuticular dilation and not within it, up to 12 rows of body hooks rather than 15 and larger eggs, 51-57 by 60-63, compared with 36-48 by 33-45.

Although the third row of cephalic hooks is relatively much smaller than the first and second rows in *L. peramelis* than in other species of *Linstowinema*, the cephalic hook sizes vary greatly between individuals and so this may not be a consistent character.

The eight *P. bougainville*, dissected to provide *L. peramelis* for this study (three of which were infected), were all registered in the SAMA in 1936, but no other collection data were given in the museum register. The collection data for AHC 4522 and 13928 are equally sparse, the information on the labels giving only the locality as possibly South Australia and captive in the Zoology Department of the University of Adelaide. Examination of the AHC records indicates that five additional bandicoots were dissected for helminths, two of which were infected with *L. peramelis*. This suggests that the prevalence

of infection in *P. bougainville* by *L. perameles* was about 38%.

Etymology

The specific name is taken from the label of AHC 4522, the material, originally registered as *Echinonema cinctum perameles*, here determined to be *L. perameles*.

Type locality

Unknown, Australia

Type host

Perameles bougainville Quoy & Gaimard, 1824

Site in host

Small intestine

Type specimens

Holotype male, AHC 30023, allotype female, AHC 30097

Linstowinema maplestoni sp. nov.

(FIGS 67-78)

Material examined

Type material: Holotype ♂, allotype ♀, from *Perameles nasuta* Dinner Creek, (17° 26'S, 146° 00'E), Queensland, 11.v.60, AHC 30094, 30095; Paratypes 4 ♂♂, 1 ♀, 2 anterior ends, 1 ♂ posterior end QM 14363/1, AHC 19763.

Other material: From *Perameles nasuta* Queensland; 2 ♂♂, no locality given, 5.ix.57, QM GL 14457, 1 ♂, 2 ♀♀, 1 ♂ fragment, Innisfail, (17° 32'S, 146° 01'E), 15.xii.59, QM GL 14356; 2 ♂♂, 2 ♀♀, southern Queensland, no date, AHC 1726.

From *Isodon macrourus* Queensland; 2 ♂♂, Mossman, (16° 28'S, 142° 23'E), 4.iii.1958, QM GL 14363/2; 2 ♂♂, 2 ♀♀, Innisfail, (17° 32'S, 146° 01'E), 22.vi.79, AHC 1726; 1 ♂, Brisbane, (27° 28'S, 151° 01'E), no date, AHC 1738; 5 ♂♂, 1 ♀, 1 anterior end, Paddington, (27° 28'S, 153° 01'E), Aug. 1955, AHC 4371; from bandicoot, no collection data, 3 ♂♂, AHC 19667.

Description

Cephalic bulb with three rows of 14 (male) (Fig. 69) or 16 (female) files of large hooks, 2nd row largest 3rd row smallest (Fig. 68); neck with 5-8 rows of tiny spines; cuticular dilation of oesophageal region bearing 11-13 rows of 14 (male) or 16 (female) files of body hooks, first and last 2 rows smallest, 7th - 9th rows largest; roots of hooks without undulations (Figs 72, 73), remainder of body with a row of up to 42 (male) or 50 (female) small spines at each annulation (Fig. 71), over whole body of female,

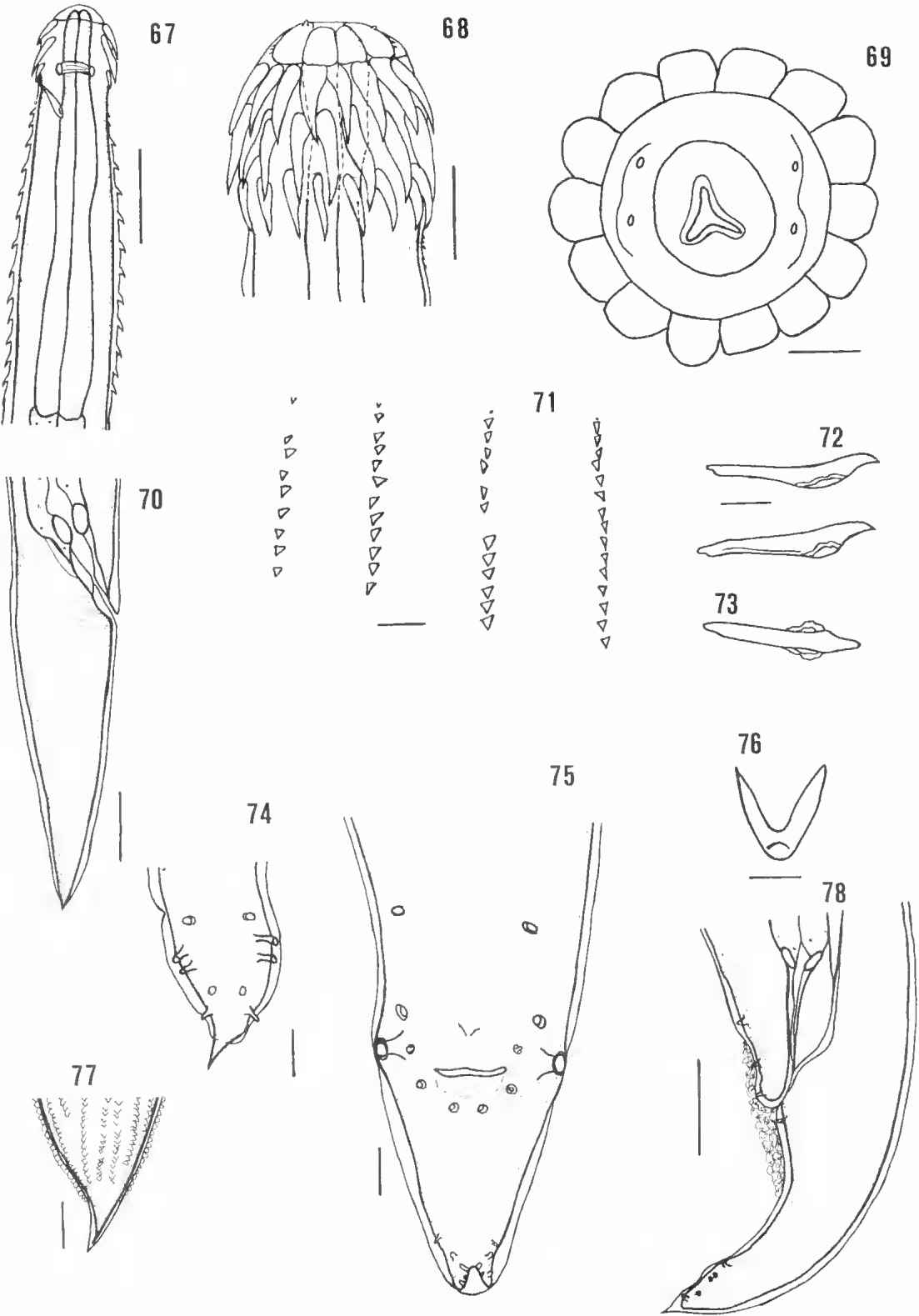
extending over $\frac{1}{2}$ dorsal surface, terminating about 400 anterior to cloaca on ventral surface of male body. Oesophagus simple, club shaped about $\frac{1}{10}$ body length terminating posterior to oesophageal cuticular dilation (Fig. 67). Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male: Length 13-23 (17.5) mm, width 475-560 (550). Cephalic bulb 285-350 (335) long by 260-310 (290) wide; cephalic hooks 1st row 117-150 (130), 2nd row 140-175 (160), 3rd row 90-130 (120) long. Oesophagus 1360-2210 (1809) long; cuticular dilation bearing 11-13 rows body hooks. Deirids 405-530 (475), nerve ring 255-300 (285), secretory-excretory pore 325-405 (360) from anterior end. Spicules equal, similar, without alae 920-1100 (1030) long, about $\frac{1}{16}$ body length. 11 pairs caudal papillae: 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively, 1 large pair lateral ad-cloacal, 2 pairs lateral pre-cloacal, 4 pairs papillae, pair phasmids well posterior to cloaca, near tail tip (Figs 74, 75). Cloacal region with small cuticular bosses, ala-like expansions absent. Gubernaculum short, simple, sub-triangular in ventral view, 60 (n=1) long (Fig. 76). Tail 305-440 (375) long (Fig. 78).

Female: Length 18-35 (28) mm, width 560-765 (670). Cephalic bulb 325-425 (362) long by 274-425 (330) wide; cephalic hooks 1st row 150-176 (160), 2nd row 170-225 (190), 3rd row 115-145 (125) long. Oesophagus 1615-3740 (2272) long; cuticular dilation bearing 12-13 rows body hooks. Deirids 405-585 (495), nerve ring 260-390 (330), secretory-excretory pore (n=2) 405-470 from anterior end. Vulva not seen. Tail 565-970 (790). Eggs not measured.

Remarks

Linstowinema maplestoni sp. nov. resembles *L. warringtoni* in having up to 13 rows of body hooks, a relatively long oesophagus and five pairs of caudal papillae on the male. It differs from *L. warringtoni* in having 11-13 (male) and 12-13 (female) compared with 9-11 (male) and 11-13 (female) rows of body hooks. The oesophagus of *L. maplestoni* extends beyond the cuticular dilation of the oesophageal region of the body whereas in *L. warringtoni* it terminates at the level of the 9th - 13th rows of body hooks. The body hooks of *L. maplestoni* are without undulating edges and those of *L. warringtoni* are with undulating edges. Male body spines extend along $\frac{1}{2}$ of the body dorsally and well above the lateral caudal papillae ventrally on *L. maplestoni* but on *L. warringtoni* they extend along $\frac{1}{3}$ of the body dorsally and almost to the lateral caudal papillae ventrally. All 6 pairs of pre-, post- and ad-cloacal papillae are the



same size on *L. warringtoni* but *L. maplestoni* has larger lateral ad-cloacal papillae. The spicules of *L. maplestoni* ($1/10$ body length) are relatively longer than those of *L. warringtoni* ($1/30$ body length). The arrangement of the papillae surrounding and anterior to the cloaca of *L. maplestoni* most closely resembles that for *L. inglesi*, i.e., with the lateral ad-cloacal pair the largest and the ventral body spines not extending to the level of the caudal papillae. *Linstowinema maplestoni* differs from *L. inglesi* in having the oesophagus extend posterior to the body hooks without undulating edges rather than an oesophagus which terminates within the cuticular dilation at about the level of rows 8-9 of the body hooks with undulating edges. Male *L. inglesi* have only three pairs of papillae on the caudal tip but *L. maplestoni* have four. Male *L. maplestoni* on average have longer tails (305-440) (375) than *L. inglesi* (150-350) (265); the body spines of *L. maplestoni* extend along $1/3$ of the body dorsally compared with almost the whole body ($7/8$) on *L. inglesi*.

Linstowinema maplestoni can be distinguished from *L. latens*, which also has the oesophagus extending posterior to the body hooks, body hooks with undulating edges and four pairs of papillae on the caudal tip, in having 11-13 (male) and 12-13 (female) rows of hooks compared with 8-10 (male) and 9-12 (female) rows of body hooks in *L. latens*. Male *L. maplestoni* have body spines extending along $1/3$ of the body dorsally and well above the lateral caudal papillae ventrally compared with *L. latens*, which has body spines extending along $1/10$ of the body dorsally and level with the most anterior lateral caudal papillae ventrally. The lateral ad-cloacal pair of papillae is largest on *L. maplestoni* compared with all 3 pairs of lateral cloacal papillae being the same size on *L. latens*. Female *L. maplestoni* have on average shorter tails (565-970) (790) than *L. latens* (790-1615) (1070).

Linstowinema maplestoni can be differentiated from *L. cinctum* in having 11-13 (male), 12-13 (female) body hooks without undulating edges compared with 13-16 (male), 14-18 (female) body hooks with undulating edges; a long oesophagus terminating posterior to the rows of body hooks, not a short oesophagus terminating at the level of the 8-11 rows of hooks. *Linstowinema maplestoni* has four pairs of caudal papillae at the tail tip, while *L. cinctum* has three; the pair of lateral ad-cloacal

papillae is the largest on *L. maplestoni* but all six pairs of cloacal papillae are the same size on *L. cinctum*. *Linstowinema maplestoni* does not have an ala-like expansion surrounding the cloaca but *L. cinctum* does; the ventral body spines of *L. cinctum* extend almost to the level of the most anterior lateral pair of pre-cloacal papillae but in *L. maplestoni* they do not; the female tail of *L. maplestoni* (565-970) (790) is shorter than that of *L. cinctum* (986-1122) (1050).

The other species of *Linstowinema*, *L. peramelis* and *L. tasmaniense*, which have body hooks without undulating edges have three pairs of caudal papillae on the tail tip. These can be further differentiated from *L. maplestoni* by the number of rows of body hooks and the relative lengths of the oesophagus. *Linstowinema peramelis* has 10-12 rows of body hooks with the oesophagus terminating at the level of the 12th row; *L. tasmaniense* has 13-15 rows of body hooks with the oesophagus terminating at the level of the 8th - 10th row and *L. maplestoni* has 11-13 rows of body hooks with the oesophagus terminating posteriorly to the 13th row. *Linstowinema peramelis* has four pairs of lateral ad- and pre-cloacal papillae, compared with three pairs on *L. maplestoni* and relatively shorter spicules ($1/10$ of body length) compared with ($1/30$). *Linstowinema tasmaniense* has three large pairs of lateral cloacal papillae compared with the one large ad-cloacal pair of *L. maplestoni*.

Because of the small number of female specimens available, none was dissected, so although eggs were seen, it was difficult to determine which were mature and therefore suitable for measuring. As a result, no measurements were made.

Linstowinema maplestoni occurs in *P. nasuta* and *L. macrourus* from Queensland and New South Wales although the examination of more hosts is required before the full extent of the geographic range of this species can be determined. In two *L. macrourus*, *L. maplestoni* occurred in mixed infections with *L. warringtoni*.

Etymology

The species is named after P.A. Maplestone, who together with W. Yorke, carried out pioneering work on the nematodes of Australian marsupials. *Echinonema maplestoni* was used on an undated museum label by Chabaud *et al.* (1980) for *Linstowinema* specimens from *L. macrourus* that were subsequently determined to be *L. warringtoni*.

Figs 67-78. *Linstowinema maplestoni* sp. nov. 67. Anterior end, optical section (lateral view). 68. Cephalic bulb (lateral view). 69. Cephalic end male, optical section at level of first row of hooks (en face view). 70. Female tail (lateral view). 71. Male, posterior body spines (ventral view). 72. Body hook (lateral view). 73. Body hook (dorsal view). 74. Male tail tip (ventral view). 75. Male tail (ventral view). 76. Gubernaculum (ventral view). 77. Female tail tip (lateral view). 78. Male tail (lateral view). Scale bars = 500 μ m 67; 200 μ m 68, 70; 50 μ m 69, 75, 77; 25 μ m 71, 72, 73, 74, 76; 100 μ m 78.

*Type host**Perameles nasuta**Type locality*

Dimer Creek (17° 26'S, 146° 00'E), Queensland, Australia

Site in host

Small intestine

Type specimens

Holotype: male, QM30094; allotype: female, QM30095

Discussion

Linstowinema warringtoni appears to be the dominant species of *Linstowinema* in eastern Australian bandicoots, being found from northern Queensland through to South Australia, including Kangaroo Island. It occurs in all extant species of *Isodon* as well as one individual of *P. nasuta*, indicating a low prevalence in this latter host species. Although *L. latens* was found in northern Queensland populations of the northern brown bandicoot, together with *L. warringtoni*, it was the only species occurring in northern brown bandicoots from the Northern Territory and the north of Western Australia, while *L. inghisi* was the only species occurring in southern brown bandicoots in the south of Western Australia.

Only one species, *L. perameles*, occurring in five of 13 *P. bougainville* examined, has been found exclusively in *Perameles* spp. and three species *L. tasmanianse*, *L. latens* and *L. inghisi* exclusively in *Isodon* spp. *L. latens* occurs in *I. macrourus*; *L. tasmanianse* and *L. inghisi* occur in *I. obesulus*. Of the other three species, *L. maplestoni* has a north-eastern distribution occurring in *I. macrourus* and *P. nasuta*, *L. cinctum* a more south-eastern distribution occurring in *I. obesulus*, *P. nasuta* and *P. gunnii*.

Further collections of material from south-eastern Australia are needed before any hypothesis on the distribution of species of *Linstowinema* can be developed. It does appear that bandicoots (*I. obesulus*) on Kangaroo Island, but not Tasmania, may have been derived from stock in which all three species (*L. warringtoni*, *L. cinctum*, and *L. tasmanianse*) were prevalent. The continuing detrimental effects of European settlement have resulted in a patchy distribution of *I. obesulus* over a reduced range (Braithwaite 1995). This decline in the host population may have affected the distribution and prevalence of species of *Linstowinema* on the mainland. The current prevalence of the three species of *Linstowinema* in bandicoots on Kangaroo Island

may reflect past prevalences of these species in bandicoots on the mainland.

The ability to trap bandicoots varies with species (their age, species and locality (Gordon & Hulbert 1989). *Perameles nasuta* is apparently more difficult to trap than species of *Isodon* (Menkhurst & Seebeck 1995). This may be the reason for the small number of *Perameles* compared with *Isodon* collected in this study (see Table 1) and in the amount of material deposited in museum collections from each host genus. A further complicating factor is the possible difference in prevalence of infection with *Linstowinema* between the two. The records of the SAMA and QM indicate that 90 *P. nasuta* have been examined for helminth parasites and, of these, only eight were infected with *L. maplestoni*, six with *L. cinctum* and one with *L. warringtoni*. Similarly, of 51 *P. gunnii* examined, only four were infected with *L. cinctum* and one with *L. warringtoni*. It is unlikely that *Linstowinema* could have been overlooked during dissection as the worms are large and can be readily detected in the small intestine. These low prevalences of infection contrast with the prevalences found for species of *Isodon* dissected in this study. Of 72 bandicoots examined, 53 were infected with *Linstowinema* spp.

A working hypothesis would be that species of *Linstowinema* are dominant in the helminth communities of *Isodon* but not in those of *Perameles*. In some areas, species of bandicoot have overlapping geographic ranges, *I. macrourus* and *P. nasuta* in the north-east, *I. obesulus* and *P. nasuta* in the south-east and *I. obesulus* and *P. gunnii* in Tasmania. Their habitat preferences within each geographic region are different, and although they may not be in strict sympatry, opportunities for incidental infection and host switching would exist. Observations from this study suggest that species of *Linstowinema* may switch from *I. obesulus* to *P. gunnii* and *P. nasuta*; from *I. obesulus* to *P. bougainville* and perhaps from *P. nasuta* to *I. macrourus*. This might account for the occurrence of *Linstowinema* in *Perameles*.

Additional collections of material from *Perameles* spp. across Australia and especially *I. obesulus* from south eastern Australia are needed to test this hypothesis.

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